

Flora Malesiana

Volume 13 – 1997

Rafflesiaceae
Boraginaceae
Daphniphyllaceae
Illiciaceae
Schisandraceae
Loranthaceae
Viscaceae



Series I – Seed Plants

Cover: *Rafflesia arnoldii* R. Br. Central Kalimantan, Bukit Raya area.
Photograph W. J. J. O. de Wilde, 1982.

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Rafflesiaceae

(W. Meijer — pp. 1–42)

Boraginaceae

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Illiciaceae & Schisandraceae

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Loranthaceae & Viscaceae

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ISBN 90-71236-33-1

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PUBLISHER'S NOTE

Starting this volume, the subdivision of the volumes into parts will be abandoned. It has appeared that hardly anywhere, not even in libraries, the parts are bound together into the thick green volumes we were familiar with in the beginning of the project. Every issue, covering one or more families, will from now on be called a volume.

ABSTRACT

Flora Malesiana. Series I, volume 13 (1997) vi + 1–454, edited by C. Kalkman et al., published by Rijksherbarium / Hortus Botanicus, Leiden, The Netherlands, under the auspices of Foundation Flora Malesiana.

ISBN 90-71236-33-1

Contains taxonomic revisions of seven Flowering Plant families for Malesia, i.e. the area covering the countries Indonesia, Malaysia, Brunei Darussalam, Singapore, The Philippines, and Papua New Guinea.

W. Meijer, **Rafflesiaceae**, pp. 1–42.

The family as here circumscribed covers the genera *Mitrastema* (1 species), *Rafflesia* (13), and *Rhizanthus* (2), all parasitic plants. The logo of Flora Malesiana is based on *Rafflesia* and is found on most of our publications.

The general part of the treatment covers 10 pages and includes paragraphs on palynology by R.W.J.M. van der Ham, and on phytochemistry by R. Hegnauer.

Family, genera, and Malesian species are described and annotated. Keys to the genera and species are given. Under *Rafflesia* a historical review of the discovery of this remarkable genus is given, and also a paragraph on *ex situ* cultivation. The name *Rafflesia titan* Jack is considered to be an incompletely known species.

One new combination is formally made, on p. 23: *Rafflesia arnoldii* R. Brown var. *atjehensis* (Koord.) Meijer, comb. et stat. nov. (Basionym: *Rafflesia atjehensis* Koord.)

Illustration is (apart from the cover photo) by 4 half-page colour photographs, 3 black/white photographs, and 8 line drawings mostly less than full-page.

H. Riedl, **Boraginaceae**, pp. 43–144.

This widespread family of over 2,000 species has only 77 species in Malesia of which 64 are indigenous, the remainder having been introduced for economical or ornamental use or as weeds. In Malesia 12 genera are represented, as follows: *Borago* (1 sp., cult.), *Bothriospermum* (1, intr.), *Carmona* (1, also cult.), *Coldenia* (1), *Cordia* (6 indig., 3 intr.), *Cynoglossum* (12 indig., 1 cult.), *Ehretia* (12), *Heliotropium* (6 indig., 5 intr.), *Myosotis* (1 indig., 1 intr.), *Omphalodes* (1, intr.), *Rotula* (1), *Tournefortia* (7), *Trichodesma* (2), *Trigonotis* (15). One dubious genus (*Crucicaryum*) is mentioned and one genus of uncertain affinities (*Pteleocarpa*) is treated fully.

The general part of the treatment covers 19 pages and includes paragraphs on vegetative anatomy by P. Baas, on palynology by R.W.J.M. van der Ham, and on phytochemistry and chemotaxonomy by R. Hegnauer.

The family, genera, and Malesian species are described and annotated. There are keys to the genera and species.

Illustration is by 14 line drawings, some of them full-page, and 4 photographs.

Tseng-chieng Huang, **Daphniphyllaceae**, pp. 145–168.

A monogeneric family, possibly closest related to *Hamamelidales* or even belonging to that order. The only genus, *Daphniphyllum*, has 16 species in Malesia.

The general part of the treatment covers 6 pages and includes paragraphs on vegetative anatomy by P. Baas, on pollen morphology by R.W.J.M. van der Ham, and on phytochemistry and chemotaxonomy by R. Hegnauer.

The genus and its Malesian species are described and annotated; a key to the species is included.

The illustration contains a distribution map of the genus and its two sections, two photographs, and five (\pm) full-page line drawings.

R.M.K. Saunders, **Illiciaceae**, pp. 169–184.

A monogeneric family, closely related to *Schisandraceae* (see next entry), the two recognized as a separate order *Illiciales*. Of the only genus, *Illicium*, 7 species occur in Western Malesia and the Philippines.

The general part of the treatment consists of 11 printed pages and includes a paragraph on pollen morphology by R.W.J.M. van der Ham, and a paragraph on phytochemistry and chemotaxonomy also covering *Schisandraceae* by R. Hegnauer.

The genus and its Malesian species are described and annotated; a key to the species is included.

Illustration is by one full-page line drawing.

R.M.K. Saunders, **Schisandraceae**, pp. 185–207.

In this family two genera are distinguished, *Kadsura* and *Schisandra*. The former has 9 species in Malesia, the latter only 2.

The general part of the treatment consists of 6 pages and contains a paragraph on pollen morphology by R.W.J.M. van der Ham. Phytochemistry and chemotaxonomy are summarized in the treatment of *Illiciaceae* (see entry above).

The family, genera, and Malesian species are described and annotated; there are keys to the genera and species.

Illustration is by two full-page line drawings.

B.A. Barlow, **Loranthaceae**, pp. 209–401.

Of this predominantly tropical family 23 genera and nearly 200 species occur in the Malesian region, as follows: *Amyema* (59 species), *Amylothea* (3), *Barathranthus* (2), *Cecarria* (1), *Cyne* (6), *Dactyliophora* (2), *Decaisnina* (21), *Dendrophthoe* (21), *Distrianthes* (1), *Elytranthe* (2), *Helixanthera* (11), *Lampas* (1), *Lepeostegeres* (9), *Lepidaria* (8), *Loranthus* (1), *Macrosolen* (24), *Papuanthes* (1), *Scurrula* (8), *Sogerianthe* (4), *Taxillus* (1), *Thaumasianthes* (1), and *Trithecanthera* (5).

The general part of the treatment consists of 20 pages and includes paragraphs on vegetative anatomy by P. Baas and L. van den Oever, and on pollen morphology by R.W.J.M. van der Ham. Phytochemistry and chemotaxonomy is treated for this family and *Viscaceae* together, see also next entry.

The family, the genera, and the Malesian species are described and annotated; for complete synonymy the reader is often referred to earlier publications by Danser or Barlow. There are keys to the genera and to the species; in the largest genus *Amyema* there are also some regional keys to the species. A key to *Loranthaceae* and *Viscaceae*, covering all Malesian taxa, is also included.

Illustration is by 32 line drawings, several full-page but often smaller, and by 15 photographs. The drawings are mostly redrawn from earlier publications.

B.A. Barlow, **Viscaceae**, pp. 403–442.

This family, nowadays usually separated from the *Loranthaceae*, has far fewer species in Malesia, viz. 26, divided over 4 genera: *Ginalloa* (6 species), *Korthalsella* (5), *Notothixos* (6), and *Viscum* (9).

The general part of the treatment covers 9 pages and includes paragraphs on vegetative anatomy by P. Baas and L. van den Oever, and on pollen morphology by R.W.J.M. van der Ham. For phytochemistry the reader is referred to the pertinent paragraph under *Loranthaceae*, where both families are considered.

The family, the genera and the Malesian species are described and annotated. There are keys to the genera and to the species. A key to *Loranthaceae* and *Viscaceae*, covering all Malesian taxa, is also included.

Illustration is by six line drawings, mostly smaller than full-page, and by 7 photographs. The drawings are mostly redrawn from earlier publications.

Index to scientific plant names of taxa treated in this volume (accepted names and synonyms) on pp. 443–452.

List of revised families in Flora Malesiana on pp. 453–455.

RAFFLESIACEAE

(W. Meijer, Lexington, U.S.A.)¹

Rafflesiaceae Dumort., Anal. Fam. Pl. (1829) 14; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 1–128; Meijer in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 2 (1993) 557–563; Hansen in Fl. Thailand 2 (1972) 182–184; in Fl. Camb., Laos & Vietnam 14 (1973) 59–64; Kiu & Wing in Fl. Reipubl. Pop. Sin. 24 (1988) 246–248; Dell in Fl. Austral. 22 (1984) 147–150.

Parasitic plants, rootless, without chlorophyll, always rich in tannins, monoecious or dioecious. *Endophytic body* as strings (chains) or plates of cells inside host plant. Flowering buds or flowering branches vascularized, bursting through the cortex of the host and terminating in a single flower or in short racemes or spikes, with series of scales (bracts) at the base of the buds. *Flowers* uni- or bisexual; perianth single (perigone), often tubular or saucer-shaped at base, in *Rafflesia* and *Sapria* the apex of the tube partly closed by a diaphragm; stamens grouped around a central column representing part of the pistil in female and bisexual flowers, often joined with that column; ovary unilocular, in general inferior but in some cases semi-inferior or superior (*Mitrastema*), with 4–6 or numerous parietal placentas. *Fruits* berry-like. *Seeds* minute, surrounded by pulp, testa hard, often thickened and pitted, embryo few-celled, undifferentiated.

DISTRIBUTION

As defined here the family is subdivided into two subfamilies with a total of nine genera and about 40 species, mainly in tropical regions, although some species occur in subtropical and even temperate parts of the world. The three genera of the tribe *Rafflesieae* of the subfamily *Rafflesioideae* are only known from Indomalesia, the other two tribes of that subfamily (*Cytineae* and *Apodantheae*) occur in America, Africa, the Mediterranean region (including Iran and Iraq), and SW Australia. The subfamily *Mitrastemoideae* has only one genus, *Mitrastema*, originally found in E and SE Asia, but later also recorded from Mexico, Guatemala, and Colombia (Meijer 1993).

HABITAT

All Malesian species are restricted to moist, evergreen, lowland or montane, primary or adjacent secondary forests.

1) With contributions by R.W.J.M. van der Ham, Leiden (palynology), and R. Hegnauer, Leiden (phytochemistry). Most original drawings are by Janis Atlee, Lexington, one by Herbert Lee, Tenom (Sabah). Photographs are from different sources as indicated. Inclusion of the colour plates was made possible through a substantial financial contribution by the author.

ECOLOGY

The ecology of *Rafflesiaceae* is of course closely interwoven with the host-parasite relationship, the chances of survival and the specific ecological requirements of the host plants, pollination efficiency, seed dispersal and dormancy, and germination chances. Between the production of about 100–150 seeds in a peppercorn-sized fruit of *Pilostyles* and a fist-size fruit of *Rafflesia* with several millions of seeds exists an enormous range of seed production per flower.

Mitrastema is most consistently reported as parasitizing the roots of *Fagaceae*: *Quercus*, *Lithocarpus*, *Trigonobalanus*, and *Castanopsis* and, if collectors' notes are accurate, occasionally adjacent tree roots of other families. All three genera of the tribe *Rafflesieae* (*Rhizanthus*, *Rafflesia*, *Sapria*) are obligate parasites of the genus *Tetrastigma* in *Vitaceae*. Where species names are mentioned in the treatment, they must be considered as preliminary, since identification of herbarium specimens is difficult and nomenclature uncertain.

Literature: Bänziger, H., Nat. Hist. Bull. Siam Soc. 39 (1991) 19–52; *ibid.* 43 (1995) 337–365.

TAXONOMY

Since Dumortier (1829) most systems of plant families of the world have treated *Rafflesiaceae* in a wide sense. Lindley (1836) and Richard (1838) considered *Cytinaceae* to be a separate family with *Pilostyles* as part of the *Rafflesiaceae* and the very closely related *Apodanthes* in the *Cytinaceae*. Van Tieghem (1890) elevated *Apodanthaceae* to the rank of family and Makino (1911) put his new genus *Mitrastema* in its own family. More recent accounts, as Thorne (1992), Beaman et al. (1992) and Meijer (1993) treat the family in a wide sense. Takhtajan et al. (1985) considered *Rafflesiaceae* *sensu lato* as a heterogeneous group, both macromorphologically and palynologically, and expressed the idea that the four tribes recognized by Harms (1935) deserve to be treated as separate families:

Rafflesiaceae: *Rafflesia*, *Rhizanthus*, *Sapria*

Apodanthaceae: *Apodanthes*, *Pilostyles*

Cytinaceae: *Bdallophyton*, *Cytinus*

Mitrastemaceae: *Mitrastema*.

Studies of ribosomal RNA of parasitic plants carried out by Dr Daniel Nickrent in Carbondale (University of South Illinois) are still preliminary but already support the removal of *Cytinaceae* from the *Rafflesiaceae* and ultimately may support the family system of Takhtajan et al. (1985). The ribosomal DNA data (Nickrent & Duff, *in press*) make it clear that the tribe *Cytineae* deserves to become a family at its own. Results on *Apodanthes* and *Pilostyles* are not yet available but it is quite possible also that they cannot easily be compared with the *Rafflesia* tribe (or family *sensu stricto*).

Solms-Laubach (1901: 7) warned not to rush to conclusions about the taxonomy and relationships of parasitic plants, which could hide their real ancestry in their strong reductions and adaptations required to survive as parasites. We can safely restrict ourselves

here to the tribe *Rafflesieae* and the subfamily *Mitrastemoideae* and leave it to future research as to how closely or distantly they might be related.

Literature: Beaman, R., et al., in: G. Ismael (ed.), Proc. Int. Conf. For. Biol. & Cons. Borneo (1992) 109. — Brown, R., Ann. Sc. Nat. 2, 1 (1834) 369–370; Trans. Linn. Soc. London 19 (1844) 221–239, 5 pl. — Dumortier, B.C.J., Anal. Fam. Pl. (1829) 14. — Harms, H., in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 243–281. — Lindley, J., Nat. Syst. Bot., ed. 2 (1836) 389–392. — Makino, T., Bot. Mag. Tokyo 25 (1911) 254–257, pl. 7. — Meijer, W., Rafflesiaceae, in: K. Kubitzki (ed.), Families & Genera of Vascular Plants, vol. 2: K. Kubitzki, J.G. Rohrer & V. Bittrich (eds.), Flow. Pl., Dicot. (1993) 557–563. — Nickrent, D.L. & R.J. Duff, Proc. 6th Parasitic Weed Symp. April 1996, Cordoba, Spain (in press). — Richard, A., Nouv. Elem. Bot., ed. 6 (1838) 1518–1520. — Solms-Laubach, H., in Engler & Prantl, Nat. Pflanzenfam. 3, 1 (1889) 274–282; in Engler, Pflanzenr. 5 (1901) 1–19, 13 illus. — Takhtajan, A.L., N. Meyer, R. & V.N. Kosenko, Bot. J. Leningrad 70 (1985) 153–162. — Thorne, R.F., Aliso 13 (1992) 365–389. — Van Tieghem, P.E.L., Traité Bot., ed. 2 (1890) 1577–1579.

PHYLOGENETIC AFFINITIES

As suggested before, considerations of this subject are still very speculative and depend on how natural the family in a wide sense really is. Takhtajan (1980) placed the two families *Hydnoraceae* and *Rafflesiaceae* in the order *Rafflesiales* in the superorder *Rafflesianae* (subclassis *Magnoliidae*). The closest relationship may well be with *Aristolochiaceae* which already Linnaeus (1753), Robert Brown (1821) and Solms-Laubach (1901) considered possible or likely. Nickrent & Duff (in press) in their preliminary work link *Hydnoraceae* with ‘paleoherbs’ like *Aristolochiaceae*. The position of *Rafflesiales* between *Santalales* and *Celastrales* in Cronquist’s system (1981) might be at variance with the evidence from floral morphology and pollen morphology. As mentioned earlier Takhtajan (1985) proposed to raise all the tribes from the system by Harms (1935) to the rank of family, based on his studies of pollen structure. Thorne (1992), however, stuck to Takhtajan’s family system of 1980 but ranked his *Rafflesianae* between *Nymphaeanae* and *Caryophyllanae*. The cladistic analysis of Beaman et al. (1992) was also based on Takhtajan’s circumscription (1980) of the family and hinges on the selection of the most primitive genus and the most closely related family: *Hydnoraceae* or *Aristolochiaceae*. The old family circumscription as followed in this flora can only be maintained when reversals are assumed.

Literature: Beaman, R., et al., in: G. Ismael (ed.), Proc. Int. Conf. For. Biol. & Cons. Borneo (1992) 109. — Brown, R., Trans. Linn. Soc. London 13 (1821) 201–234, 8 pl. — Cronquist, A., Integr. System Class. Flow. Plants (1981) 703–704. — Harms, H., in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 243–281. — Linnaeus, C., Spec. Pl. (1753) 442. — Nickrent, D.L. & R.J. Duff, Proc. 6th Parasitic Weed Symp. April 1996, Cordoba, Spain (in press). — Solms-Laubach, H., in Engler, Pflanzenr. 5 (1901) 1–19, 13 illus. — Takhtajan, A.L., Bot. Rev. 46 (1980) 225–359. — Takhtajan, A.L., N. Meyer, R. & V.N. Kosenko, Bot. J. Leningrad 70 (1985) 153–162. — Thorne, R.F., Bot. Rev. 58 (1992) 225–348.

VEGETATIVE MORPHOLOGY AND ANATOMY

The vegetative parts are a kind of tissue mass often compared with fungal mycelia. The cells have remarkable large nuclei and form the so-called endophytic system within the

stems and roots of the host plants, especially inside the living bark close to the cambium of the host. From there, special strings (so-called sinkers) can penetrate through rays of the host into the deeper lying xylem, while these cell strings inside the host cambium in general keep pace with the secondary growth of the host. In *Pilostyles thurberi* the endophytic body stays at a uniform distance from the apical meristem of the host (Rutherford 1970), in the *Cytineae* generally near the ground level and in the *Rafflesieae* in the roots as well as high on stems, though in general close to the ground. When the host cambium is reactivated, it may succeed to put a xylem layer on top of the parasite tissues. In general the parasite can migrate through the rays into the new host tissues, as described by Forstmeier et al. (1983) for *Cytinus*.

The simple cell strings do not contain vascular tissues; in many genera these occur mainly in cell cushions from which flowering structures originate, connecting ultimately with the staminal or ovary structures.

Solms-Laubach (1869) described the situation in *Cytinus* where the parasite forms a kind of tissue sleeve between cambium and xylem of the *Cistus* host root. In a rhythmic way, parts of the parasite tissue are covered by xylem layers, apparently and for unknown reasons turning the cambium activity off from time to time. The resulting more mature closed cylinder sleeve of the parasite consists of a cambium and two surrounding layers of tissue: an inner medullary and outer cortical plate. In the latter many irregular weak vascular bundles occur. Flowering structures originate inside swollen parenchyma tissues and cause gall-like growth above connections with the vascular bundles of the host plant, in general at least 2–3 years after the first infection of the host. The host tissues are filled with starch at this place except in a few cell layers close to the parasite tissue. These and similar situations were observed by Cartellieri (1926) in *Rhizanthus*, Brown (1912) in *Rafflesia manillana*, Haak (1889), Schaar (1898) and Hunziker (1920) in *Rafflesia patma*, Endriss (1902) in *Pilostyles ingae*, Rutherford (1970) in *Pilostyles thurberi* and Meijer & Behnke (unpubl.) in *Rhizanthus*, while the old classical study by Solms-Laubach (1875) is still of value. If the family is polyphyletic we are dealing here with remarkable convergences in growth morphology.

Kuijt et al. (1985) discovered sieve elements in the endophytic body of *Pilostyles thurberi*, apparently in a discontinuous system which they considered to be a vestigial cell type. In older studies such elements were in general overlooked.

Weak vascular tissues are reported from the endophytic bodies of species of *Pilostyles*. Floral tissue cushions contain rings of concentric vascular bundles in *Rafflesia* and *Rhizanthus*.

Most of the tissues are parenchymatous and these cells also never contain starch. In all genera the parenchymatous tissues are rich in tannins.

Stomata are known from scales of *Pilostyles* and *Cytinus* and also from *Rafflesia* and *Rhizanthus* (see Cammerloher 1920). Glandular hairs are known from the bracts of *Cytinus* and also in some species from the perigone. The function of the so-called ramenta, the outgrowths inside the flower tubes of species of *Rafflesia* and from the upper part of the diaphragm of *Sapria* is still unknown; their different forms have diagnostic taxonom-

ic value (Winkler 1927). The osmophoric and nectarial structures of the family still need more comparative anatomical studies.

Literature: Brown, W. H., Philipp. J. Sc., Bot. 7 (1912) 209–224, pl. 12–21. — Cammerloher, H., Oesterr. Bot. Zeitschr. 69 (1920) 153–164, t. 3. — Cartellieri, E. von, Bot. Archiv 14 (1926) 284–311, 7 pl. — Endriss, W., Flora, 91, Erg. Band (1902) 209–236, t. 20. — Forstmeier, L., F. Weberling & H.C. Weber, Beitr. Biol. Pflanzen 58 (1983) 299–312. — Haak, J., Observ. Rafflesias (1889) 14 pp. — Hunziker, J., PhD Thesis Freiburg (1920). — Kuijt, J., D. Bray & L.R. Olson, Canad. J. Bot. 63 (1985) 1231–1240. — Rutherford, R.J., Aliso 7 (1970) 263–288. — Schaar, F., Sitzungsber. K. Akad. Wiss. Wien, Math.-Naturw. Kl. 107 (1898) 1039–1056. — Solms-Laubach, H., Bot. Zeitung 27 (1869) 185–190; Abh. Naturf. Ges. Halle, 13, 3 (1875) 40 pp., t. 24–27. — Winkler, H., Planta 4 (1927) 1–97, t. 1.

FLOWER MORPHOLOGY

Only in the genus *Bdallophyton* do the flowering structures (inflorescences) have a well developed long axis. In all other genera they are more or less fascicles or very short uniflowered shoots, surrounded by a few whorls of scaly dark brown or blackish leaves. In *Rafflesia* and *Rhizanthus* there are in general 3 whorls of 5 scales (bracts), in *Pilostyles* the whorls are 3–6-merous. *Apodanthes* has a regular structure of 2 outer bracts, 4 calyx-like bracts followed by 4 perigone lobes and an ovary with 4 placentas. Only in the tribus *Cytineae* inflorescences are developed like racemes, spikes or umbels, sometimes with bracts and bracteoles.

Flowers are in general unisexual. In *Rhizanthus zippelii* unisexual flowers occur besides bisexual ones. *Bdallophyton oxylepis* has bisexual flowers and *B. americanum* unisexual ones on different plants; *Mitrastema* is always bisexual and protandrous.

Perigones can be partly tubular at their bases and the lobes are imbricate (*Rafflesia*) or valvate (*Rhizanthus*). *Rafflesia* and *Sapria* possess as unique organ the diaphragma. Staminal structures always have the thecae interconnected in a ring like in *Hydnoraceae*, though never in phalanges, and are in various ways connected with the central column. In some cases in *Pilostyles* they occur in 2–4 rings. The detailed anatomy of the anthers in various genera shows also some variation (see Fig. 1).

Literature: Koorders, S. H., Bot. Overz. Raffles. Ned.-Indië (1918) 206–215. — Meijer, W., in: K. Kubitzki (ed.), Families & Genera of Vascular Plants, vol. 2: K. Kubitzki, J. G. Rohrer & V. Bittrich (eds.), Flow. Pl., Dicot. (1993) 557–563.

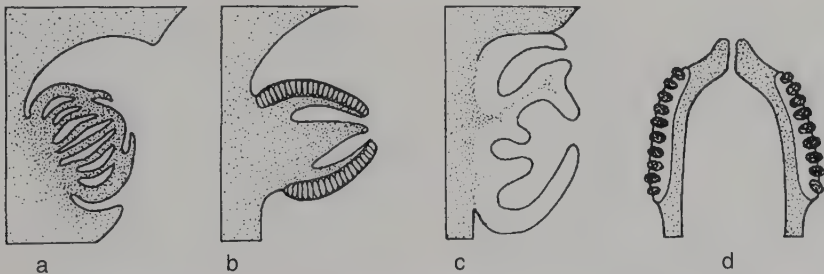


Fig. 1. Comparison of anther structures in different genera, schematic. a. *Rafflesia*; b. *Sapria*; c. *Rhizanthus*; d. *Mitrastema*. Drawing Janis Atlee.

PALYNOLOGY

(R.W.J.M. van der Ham)

The most detailed account of *Rafflesiaceae* pollen is that of Takhtajan et al. (1985), which includes light and electron microscopic data of 25 species belonging to 7 genera. Others deal with one or a few species only. Straka (1978), Straka & Friedrich (1984) and Valdes et al. (1987) provide pollen descriptions with light and scanning electron micrographs of a few species of the most diverse genus *Cytinus*.

Pollen of the four tribes, as recognised by Harms (1935), is so different that it cannot be easily covered in a single description. Pollen grains of the *Rafflesieae* (*Rafflesia*, *Rhizanthus*, *Sapria*) are subspherical to ellipsoidal, 12–21 µm large monads, with one distal pore or short colpus. The exine consists of a lamellate endexine (2–4 sublayers) and a loosely attached, sporopolliniferous perine-like outer layer. Pollen of *Rafflesia arnoldii* also has a homogeneous ectexine. The ornamentation is finely to very coarsely rugulate-verrucate.

Pollen grains of the *Apodanthaeae* (*Pilostyles*; pollen of *Apodanthes* and *Berlinianche* still unknown) are prolate ($P \times E = 18\text{--}28 \times 10\text{--}20$ µm), tricolpate monads. The colpi are long and narrow. The exine consists of a homogeneous ectexine and an endexine that is often lamellate in its outer part. Locally the ectexine may be differentiated into tectum, columellate infratectum and foot layer. The ornamentation is \pm psilate.

Pollen grains of the *Cytineae* (*Cytinus*, *Bdallophyton*) are monads (*Cytinus*, *Bdallophyton*), or they are united in tetragonal, rhomboidal or tetrahedral, calymmate or acalymmate tetrads or, sometimes, dyads (*Cytinus*). The grains are subspherical to ellipsoidal, subiso- to heteropolar, 11–24 µm large, with $2\text{--}4 \pm$ equatorial pori or short colpi (*Cytinus*), or (2) 3–4 long meridional colpi (*Bdallophyton*). The exine consists of a tectum, a distinct columellate infratectum and a nexine. The endexine is very thin, and recognisable only in the apertural areas. *Cytinus* pollen is sometimes semi- or intectate. The ornamentation is verrucate, perforate or \pm reticulate in *Cytinus*, and perforate in *Bdallophyton*.

Pollen grains of the *Mitrastemoneae* are triangular-ellipsoidal, 25–28 µm large monads, usually with 3 equatorial(?) pores. The exine mainly consists of endexine, which is lamellate near the apertures. The ectexine is represented by small isolated verrucae. The ornamentation is psilate to scabrate.

The heterogeneity of *Rafflesiaceae* pollen led Takhtajan et al. (1985) to the concept that the family should be split into four natural families: *Rafflesiaceae* sensu stricto, *Apodanthaceae*, *Cytinaceae* and *Mitrastemaceae* (see also p. 2). They did not indicate if these families form a monophyletic taxon. The single distal (monosulcate, ulcerate) aperture and the throughout lamellate endexine of the pollen of the *Rafflesieae* – primitive features within the dicotyledons – suggest that this group belongs to the subclass *Magnoliidae*, near the *Aristolochiaceae* (Takhtajan et al. 1985). With respect to the monophyly of the *Rafflesiaceae* sensu lato, it is important to determine whether the (2-) 3- (4-)porate and -colpate pollen types of the other tribes are ‘monosulcate-derived’ or ‘tricolpate-derived’ (Walker & Doyle 1975), and also if the monosulcate/ulcerate aperture type of the *Rafflesieae* represents the original, primitive state of the aperture in *Magnoliidae* pollen.

References: Harms, H., in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 243–281. — Straka, H., Pollen et Spores 20 (1978) 162–163. — Straka, H. & B. Friedrich, Trop. Subtrop. Pflanzenwelt 51 (1984) 545–546. — Takhtajan, A. L., N. R. Meyer & V. N. Kosenko, Bot. J. Leningrad. 70 (1985) 153–162. — Valdes, B., M. J. Díez & I. Fernández, Atlas polínico de Andalucía Occidental (1987). — Walker, J. W. & J. A. Doyle, Ann. Missouri Bot. Gard. 62 (1975) 664–723.

POLLINATION

The foetid smell of the flowers of *Rafflesia* attracts carrion-flies of the genus *Lucilia* (Docters van Leeuwen 1929; Ross in Meijer 1985; Beaman et al. 1988; Bänziger 1991). The smell is produced by fresh flowers, especially during sunny warm periods of the day. Beaman et al. suggested they observed green flies in action in *Rafflesia* at the upper part of the gullies in the column leading to the anther cavities between rows of hairs (Meijer 1985). The actual act of pollination is well illustrated by Bänziger (1991), see Fig. 2. Still nobody has fully documented with a video camera what the flies do: laying eggs, collecting nectar (Haak 1885) or just using the carpet of ramentae as a mating ground (as insects do inside the odorous inflorescences of aroids: Croat, verbal comm.). The flies carry the pollen on their backs but have not been observed to use it as food. The actual source area (osmophore) of the bad odour is also still not yet known. Bänziger (1991) suggested from his own observations that the smell originates from the perigone lobes. Maybe the stomata described by Cammerloher (1920) have a function after all.

Douglas Warren Stevens noticed during his exploration of Nicaragua a faint smell from the flowers in *Bdallophyton americanum* (verbal comm.) and Rutherford (1966) reported this also from the masses of flowers of *Pilostyles thurberi*, both genera which like *Cytinus* and *Mitrastemon* also produce nectar. Honeyeater birds use flowers of *Mitrastemon* in New Guinea as nectar source (Beehler 1994).

Bänziger (1995: 352–356) gave interesting new data on solidification of the liquid pollen of *Rhizanthus* on the back of pollinating insects and reliquefying by profuse stigmatic fluid and viability over a period of 3 weeks. He also gave details with more recent names of the pollinating carrion flies now classified as *Calliphoridae*.

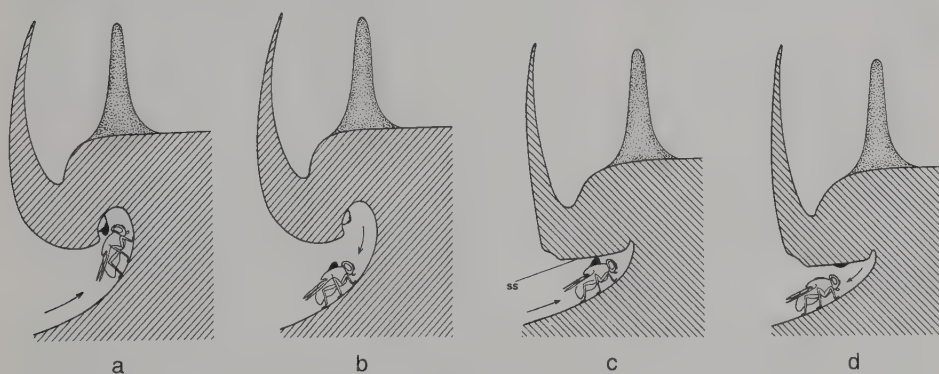


Fig. 2. Schematic pictures of flies picking up pollen in a male flower of *Rafflesia kerrii* (a, b) and striking it off on the stigma of a female flower (c, d). ss: stigmatic surface. Reproduced with permission from Bänziger (1991).

References: Bänziger, H., Nat. Hist. Bull. Siam Soc. 39 (1991) 19–52; *ibid.* 43 (1995) 337–365. — Beaman, R., et al., Amer. J. Bot. 75 (1988) 1148–1162. — Beehler, B.M., Biotropica 26 (1994) 459–461. — Cammerloher, H., Oesterr. Bot. Zeitschr. 69 (1920) 153–164, t. 3. — Docters van Leeuwen, W.J., Trop. Natuur 18 (1929) 43–45. — Haak, J., Weekbl. Pharmacie 3 (1885) 19 pp., 2 pl. — Meijer, W., Nat. Geogr. 168 (1985) 136–140. — Rutherford, R.J., PhD Thesis Claremont Grad. School, USA (1966).

LIFE CYCLE

If we assume that the species of *Rafflesia* do not vary much in their life cycles we can reconstruct from data supplied by Teijsmann (1856a, b, 1858), Docters van Leeuwen (1929), Meijer (1958 and recent unpublished observations) that the total life cycle in that genus from seed to seed is about 3–4.5 years. New experiments started in Bogor and in temperate greenhouses in 1991 with seeds of *R. gadutensis* from West Sumatra, so far have not produced results. The life cycles of other genera of this family in Malesia are still incompletely known, except that Bänziger (1995) observed for buds of *Rhizanthus lowii* (*Rh. zippelii* sensu Bänziger) that it took an estimated 200–255 days from the point of breaking through the host tissue at a circumference of 3.7 to 4.1 cm to opening of the flower.

References: Bänziger, H., Nat. Hist. Bull. Siam Soc. 43 (1995) 337–365. — Docters van Leeuwen, W.J., Trop. Natuur 18 (1929) 43–45. — Meijer, W., Ann. Bogor. 3 (1958) 33–44. — Teijsmann, J.E., Nat. Tijds. Ned. Indië 12 (1856a) 279–281; Hook. J. Bot. & Kew Gard. Misc. 8 (1856b) 371–374; Ann. Hortic. Bot., Fl. Jard. Roy. Pays-Bas (1858) 27–30.

FRUITS AND EMBRYOLOGY

Field observations in 1981 and 1983 in the Ulu Gadut area near Padang, West Sumatra have shown that ripening of fruits of *Rafflesia gadutensis* takes about 8 months. Two fruits were monitored for periods of 6–7 months and the eldest had ripe seeds in February 1984. Meijer's guide Satar, who was monitoring this fruit below his hut, mentioned that it was visited by a 'tupai kuning' (most likely a tree shrew), the same species which was eating his young chickens. In Sumatra as well as Borneo we noticed male buds being opened by squirrels or/and tree shrews and it looks as if one shrew sitting on the exit of such a vandalized bud was captured on the lens on Kinabalu near Poring; see Attenborough (1995). It sits on a bud not at the entrance of a flower as the legend in the book asserts. The holes made are too small for most squirrels.

From a very obscure report by R.H.C.C. Scheffer in a letter to Solms-Laubach [cited in Solms-Laubach (1875: 27)] it might appear that actual pollination is not necessary for fruit set. Scheffer wrote to Solms (translated): "Only one of the buds made it into a flower, only 3 years after the inoculation. Notwithstanding this was a female one, and without having a male flower nearby it still developed seeds. These were used to infect another plant of *Cissus scariosa* [= *Tetrastigma leucostaphylum*] and this was successful."

Solms asserts that Scheffer suspected that the rudimentary anthers might have produced some pollen. That is very unlikely. Meijer's unpublished field observations showed that unfertilized female flowers, several months after flowering, had produced no seeds with embryos. Ovaries with very little pollination may be stimulated to grow

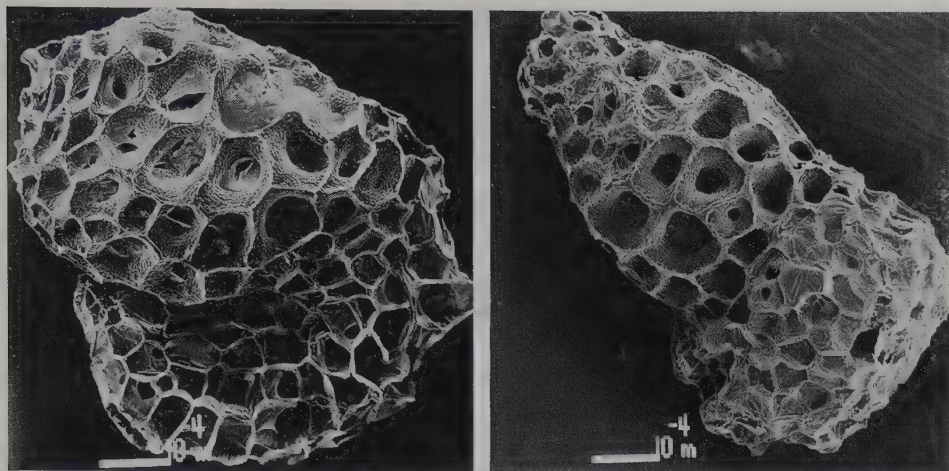


Fig. 3. Mature seeds of *Rafflesia rochussenii* Teijsm. & Binn. (left) and *Rhizanthus zippelii* (Blume) Spach (right). Scanning electron micrographs F. Bouman, courtesy Hugo de Vries-Laboratorium, University of Amsterdam.

into fruits, but they can be full of seeds without embryos as observed from a fruit of *Rafflesia keithii* outside the Kinabalu National Park, August 1993 (seeds tested by F. Bouman, Amsterdam). Possibly there were other flowers of *Rafflesia* open in the garden or on Mount Salak about 120 years ago, to account for Scheffer's observations. Real parthenocarpy of *Rafflesia* has never been proven.

Ovule and seed development stages have been studied for *Rafflesia* and *Rhizanthus* (Solms-Laubach 1898; Ernst & Schmid 1913). Pollen tetrads form according to the succedaneous system; the tapetum of anthers consists of 2 or 3 layers of cells. The stigma is in *Rafflesia* and *Rhizanthus* situated in a ring around the rim of the column disk, often more or less papillose; the ovary shows in these genera a maze of placental plates which fill the ovary cavity. For the development of the embryosac see Ernst & Schmid (1913) and Olah (1960). The outer integument is reduced. Ovaries grow into berry-like fruits, with whitish pulpa around the seeds. The seeds (Fig. 3) are small and with hard scales [see Harms (1935: 255) and Bouman & Meijer (1994)]. *Rafflesia patma* has a 2-cell suspensor and an embryo consisting of 3–5 layers of 2–4 cells, often only 6 cells in total. Endosperm is nuclear and consists of 30–40 cells in *R. patma*. Endosperm and embryo mostly contain oil, see also Schuerhoff (1926: 526). *Mitrastema* also has cellular endosperm, but ovules with only one integument.

References: Attenborough, D., *The private life of Plants* (1995). — Bouman, F. & W. Meijer, *Pl. Syst. Evol.* 193 (1994) 187–212. — Ernst, A. & E. Schmid, *Ann. Jard. Bot. Buitenzorg* II, 12 (1913) 1–58, t. 1–8. — Harms, H., in Engler & Prantl, *Nat. Pflanzenfam.*, ed. 2, 16b (1935) 243–281. — Olah, L. V., *Bull. Torrey Bot. Club* 87 (1960) 406–416. — Schuerhoff, P. N., *Zytol. Blütenpfl.* (1926). — Solms-Laubach, H., *Abh. Naturf. Ges. Halle* 13, 3 (1875) 40 pp., t. 24–27; *Ann. Jard. Bot. Buitenzorg* 9 (1891) 184–246, 28 pl.; *ibid.*, Suppl. 2 (1898) 11.

DISPERSAL

Watanabe (1933, 1936) assumed long range seed dispersal of *Mitrastema* by birds. Observations of jungle walkers working for Meijer (1958, 1983) at the sites of *Rafflesia* in West Sumatra showed that ground squirrels and tree shrews like to eat the contents of the white pulpy ripe fruits of these plants. These observations have been confirmed now by Emmons, Jamili Nais and Ali Briun (1991) and documented with colour photographs from a hide erected in August 1989 near a fruit of *Rafflesia keithii* on Mt Kinabalu. The fruits of *Rhizanthes* also have white pulp, but they are hidden under the old perigones and predation has never been observed yet.

In analogy with other root and stem parasitic plants it is assumed that only disturbance and damage to the organs of the host can deliver the signal for seeds in contact with them to germinate (Bouman & Meijer 1994).

References: Bouman, F. & W. Meijer, Pl. Syst. Evol. 193 (1994) 187–212. — Emmons, L., et al., Biotropica 23 (1991) 197–199. — Meijer, W., Ann. Bogor. 3 (1958) 33–44, fig.; Essays on Rafflesiaceae (1983) 1–20. — Watanabe, K., Bot. Mag. Tokyo 47 (1933) 798–805; J. Jap. Bot. 12 (1936) 603–618.

PHYTOCHEMISTRY

(R. Hegnauer)

This mainly tropical family of parasitic plants is badly known at present from a chemical point of view (see Hegnauer 1973, 1990). *Cytinus hypocistis* yielded isoterchebin, an ellagitannin, as its yellow pigment and pelargonidin 3-galactoside and petunidin 3-glucoside as red flower pigments. The sole crystalline compound isolated from acetone extracts of *Psilostyles thurberi* turned out to be sucrose. Pollination biology of *Rafflesiaceae* is still poorly known. Recent observations with *Rafflesia pricei* suggest that optical and olfactory mimicry may offer the clue. Flower pigments and odorous principles emanated from flowers attract carrion-flies; they seem not to be compensated for their pollination activities by nurture or suitable breeding sites. Most authors are convinced that *Rafflesiaceae* belong to or are affiliated with *Polycarpicae* sensu Wettstein. However, synthesis and accumulation of ellagitannins do not favour such an assumption, because polymeric proanthocyanidins (i.e. 'condensed tannins') are the characteristic tannin-like metabolites of *Polycarpicae*. In this respect *Rafflesiaceae* are similar to *Nymphaeaceae* s.str. which produce ellagitannins and possibly *Cabombaceae* which produce gallic acid and probably gallotannins. Therefore it is noteworthy that Takhtajan (1980) has *Aristolochiales*, *Rafflesiales*, *Nymphaeales* (*Cabombaceae*, *Nymphaeaceae* s.str. and *Ceratophyllaceae*) and *Nelumbonales* as numbers 5–8 in his subclass *Magnoliidae*, and that in Thorne's (1992) classification *Aristolochiaceae* are incorporated in *Magnolianaes*—*Magnoliales*—*Magnoliidae* and the superorders *Nymphaeanae* and *Rafflesianae* immediately follow *Magnolianaes*. *Nelumbonales* and *Ceratophyllales* are treated by Thorne as orders of *Magnolianaes*. Synthesis and accumulation of gallo- and ellagitannins may have evolved in a number of taxa now considered as outgroups of true polycarps.

References: Hegnauer, R., Chemotaxonomie der Pflanzen 6 (1973) 9; 9 (1990) 314–315. — Takhtajan, A.L., Outline of the classification of flowering plants (*Magnoliophyta*), Bot. Rev. 46 (1980) 225–359. — Thorne, R.F., Classification and geography of flowering plants, Bot. Rev. 58 (1992) 225–348.

KEY TO THE GENERA

- 1a. Ovary superior, staminal structure a tube surrounding the pistil with a series of anthers above each other. Host plants in general *Fagaceae* **Mitrastema** (p. 11)
- b. Ovary inferior or half-inferior, staminal structures different. Host plants species of *Tetrastigma* (*Vitaceae*) 2
- 2a. Mature flower buds oblong. Perigone without diaphragm, lobes 16–18, valvate, ending in bayonets (elongate stiff pointed appendages), which are hidden in a cavity at apex of the column while flowers are in the bud stage . **Rhizanthus** (p. 37)
- b. Mature buds more or less globular. Perigone with a diaphragm, the lobes imbricate, 5–10 3
- 3a. Perigone lobes 5; ramenta only inside the flower tube **Rafflesia** (p. 13)
- b. Perigone lobes 10; ramenta on top of the diaphragm . . . **Sapria** (Continental Asia)

MITRASTEMA

Mitrastema Makino, Bot. Mag. Tokyo 23 (1909) 326 ('*Mitrastemma*'). — *Mitrastemon* Makino, Bot. Mag. Tokyo 25 (1911) 225, orth. mut., nom. inval.; Jochems, Rec. Trav. Bot. Néerl. 259 (1928) 203; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 274; Yamamoto, Bot. Mag. Tokyo 50 (1936) 539; Watanabe, J. Jap. Bot. 13 (1937) 154; Matuda, Bull. Torrey Bot. Club 74 (1947) 133; Meijer in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 2 (1993) 560; Meijer & Veldkamp, Blumea 38 (1993) 221–229. — Type species: *Mitrastema yamamotoi* Makino ('*Mitrastemma*').

Chlorophyll-less endoparasites with fungus-like endophytic body. Stems unbranched. *Leaves* scale-like, decussate. *Flowers* solitary, terminal, bisexual. *Perianth* much reduced, collar-shaped. *Stamens* numerous, completely connate into a tube, below the sterile apical part with several vertical series of rings of c. 10 anthers each; pollen dicolpate, with reduced ectexine. *Ovary* superior, 1-locular, ovules numerous, anatropous, uni-temic. *Fruit* a slightly woody, berry-like capsule, horizontally dehiscent. *Seeds* sticky, testa hard. — **Fig. 4, 5.**

Distribution — Two species, one in Asia, from Japan to Taiwan, Yunnan, Bhutan, Assam, Indo-China, and *Malesia*: Borneo, Sumatra and New Guinea; a second, very closely related species (?) from Chiapas (Mexico) to Alta Vera Paz (Guatemala) and Antioquia (W Colombia).

Habitat — In montane oak-chestnut forests, altitude 1400–2000 m.

Ecology — The Asian species parasitic on roots of *Fagaceae*, probably the American species too. Pollination by insects and birds, seed dispersal most likely by birds and small mammals.

Notes — 1. According to Matsuura, J. Fac. Sc. Hokkaido Imp. Univ. V, Bot. 3 (1935) 189, and Watanabe, J. Jap. Bot. 12 (1936) 769, f. 26P, the chromosome number is $n = 20$.

2. About the orthography of the genus name, see Meijer & Veldkamp, l.c.

Mitrastema yamamotoi Makino

Mitrastema yamamotoi Makino, Bot. Mag. Tokyo 23 (1909) 326, fig.; P. Royen, Nova Guinea, Bot. 14 (1963) 243–245, pl. 17; Hansen, Bot. Tidsskr. 67 (1972) 149; in Fl. Camb., Laos & Vietnam 64 (1973) 62, t. 9; Tang Shui Liu & Ming You Lai in Fl. Taiwan 2 (1976) 582, t. 414; Meijer & Veldkamp, Blumea 38 (1993) 227. — Syntypes: *Tashiro s. n.*, *Bando s. n.*, *Yamamoto s. n.* (TI holo), Japan, Kyushu.

Mitrastemon sumatranum Nakai, Icon. Pl. As. Or. 4 (1941) 338, t. 113 ('*sumatranus*'). — Type: *Jochems s. n.* (TI holo), Sumatra, Karo Mts.

For more complete synonymy and references, see Meijer & Veldkamp, l.c.

Plants about 2.5–15 cm long and up to 3 cm in diameter. Basal part a corky pustular cupule, up to c. 2 cm high and in diameter, the margin an irregularly low lobed rim; stems 5–15 mm diam. *Leaves* (also called bracts or scales) in 3–4(–7) decussate whorls, increasing in length from the base of the plant upwards, broadly to narrowly ovate, at apex blunt-rounded, (4–)10–20(–28) by (5–)10–15(–25) mm, cream (turning ebony) coloured with brown spots, the lowest often purplish brown. *Flowers* up to 20 mm long, with a foetid smell. *Perigone* 5–10 by 6–17 mm, truncate or slightly 4-lobed. *Staminal tube* tubular, wide and globose in the basal part, 14–20 mm long, the minute anthers in a 2–5 mm broad ring in the upper part, the whole collar early caducous. *Ovary* ellipsoid, c. 8 by 3 mm, style ovoid-ellipsoid, 2–8 by 3–6 mm, stigma 2–5 by 4–6 mm; 8–15 radial placentas. *Fruit* up to c. 20 by 10 mm, opening along a horizontal ring about halfway. *Seeds* c. 0.25 mm diameter, with a small funicle, yellowish or dark brown. —

Fig. 4, 5.

Distribution — India, Thailand, Cambodia, Vietnam, China (Yunnan), Japan, Taiwan; *Malesia*: Sumatra (Aceh, East Coast), Borneo (Sabah: Mt Kinabalu; Sarawak: 4th Division), Papua New Guinea (W and E Highlands, Morobe, Milne Bay Provinces).

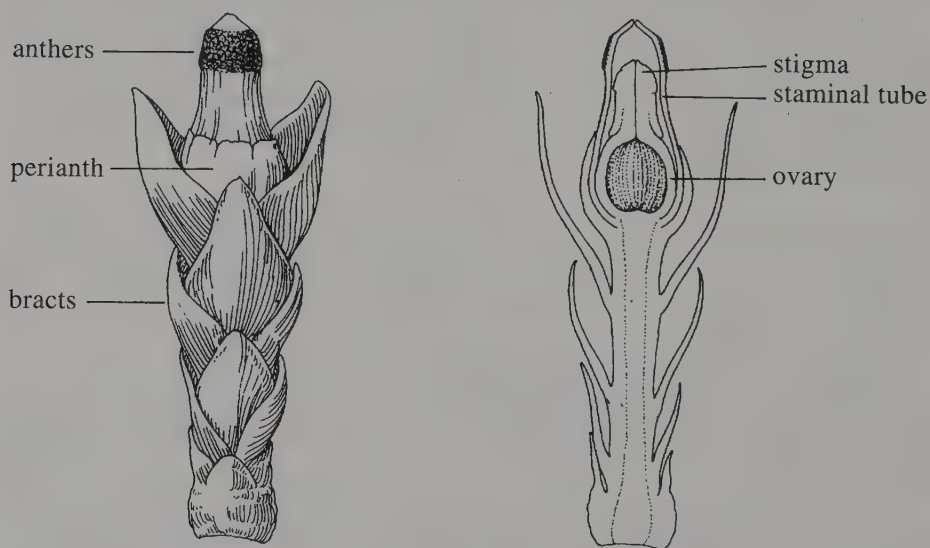


Fig. 4. *Mitrastema yamamotoi* Makino. Full open flower, habit and length section, with indication of flower parts. True size up to 15 cm high. Drawing by Janis Atlee after the type description by Makino.



Fig. 5. *Mitrastema yamamotoi* Makino. Dried flower on host. Sumatra, Berastagi, coll. by A. Stomps. Photo by F.D. Boesewinkel, Amsterdam.

Habitat — Montane oak forests, at altitudes of 1400 to 2000 m.

Ecology — In Malesia *Mitrastema yamamotoi* is in general reported as a root parasite of *Fagaceae*: *Castanopsis*, *Lithocarpus*, *Quercus*, *Trigonobalanus* [Akuzawa, Paras. Pl. Magaz. 13 / 4 (1985) 23], but also on species of other families. Flowering is reported on Mt Kinabalu around April, the fruits ripening in about 4 months [Akuzawa, Paras. Pl. Magaz. 15 / 1 (1986) 26].

RAFFLESIA

Rafflesia R. Br., Trans. Linn. Soc. 13 (June 1821) 201; Jack, Appendix Descr. Mal. Pl. 1 (July 1821); Jack ex Hook., Comp. Bot. Mag. 1 (1835) 259, pl. 14; R. Br., Trans. Linn. Soc. 19 (1844) 221; Solms-Laubach in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1889) 279; in Engl., Pflanzenr. 5 (1901) 8; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 259; Meijer, Blumea 30 (1984) 209; in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 2 (1993) 561. — Type species: *Rafflesia arnoldii* R. Br.

Parasitic plants, endophytic body growing like a thallus inside the woody stems and roots of species of *Tetrastigma* (*Vitaceae*). *Flower buds* sessile, first protruding as a corky swelling with hexagonal patches, the corky base remaining as a cup-shaped body (cupule) below the scales on the flowering sessile shoot. *Scales* (bracts) in a series of 3 whorls of 5 scales, imbricate, at first appearance white, but turning black or dark brown

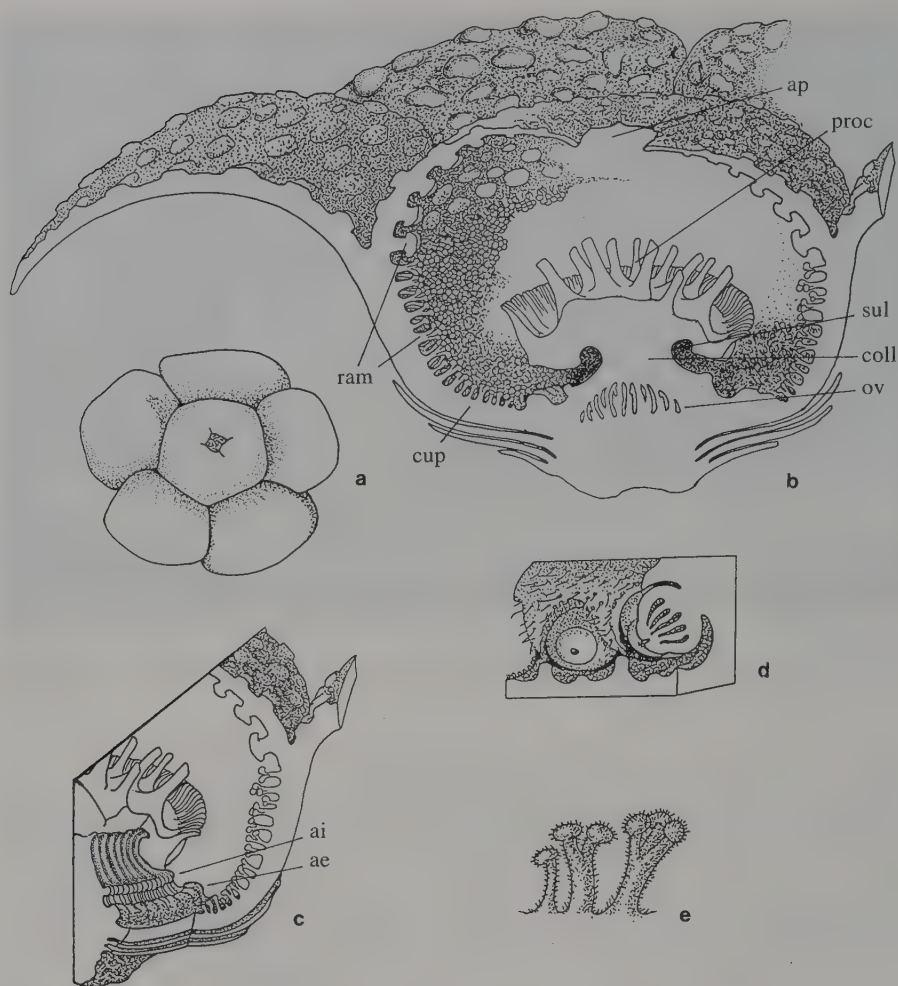


Fig. 6. *Rafflesia micropylora* Meijer. a. Flower with the small aperture in the diaphragm clearly showing; b. female flower, halved lengthwise, showing central column (ap: aperture in diaphragm; coll: collum, neck of column; cup: cupula, perigone tube; ov: ovary; proc: processi on apex of disc; ram: ramenta on inside of cupula and diaphragm; sul: sulcus under disc); c. side view of the column of a female flower showing outer and inner annulus (ae: annulus exterior, ai: annulus interior); d. section through male flowers, anther in longitudinal section and seen from lower side of the overhang of the 'corona' of the disc towards the sulcus; e. details of ramenta, often branched and with swollen apices. Drawings by Janis Atlee (a, b, d, e) and Herbert Lee (c), made from colour slides by W. J. de Wilde and drawings from BO.

after exposure, with prominent veins, inner gradually larger. *Flowers* (see Fig. 6) unisexual, female ones with rudiments of anthers. *Perigone lobes* 5, imbricate, reddish, often with white warts, inserted around an annular, horizontal, pentagonal, central diaphragm which has a more or less round opening (orifice) in the centre (see Fig. 7, 8).

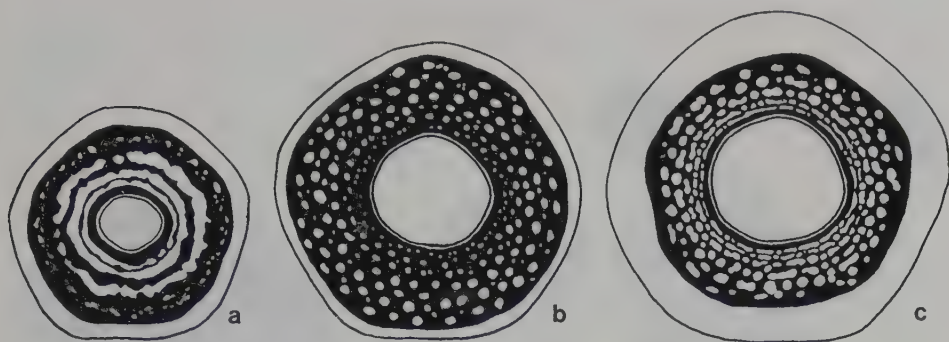


Fig. 7. *Rafflesia* spp. Semidiagrammatic representation of the diaphragms of: a. *Rafflesia hasseltii* (4 concentric rings, not of warts but at same level as surrounding tissue), b. *Rafflesia kerrii* (7 concentric rings of very small white warts), and c. *Rafflesia keithii* (5 concentric rings of white warts). Drawing by Janis Atlee.

Base of perigone tube and adjacent zone of diaphragm (or the entire diaphragm) covered with variably shaped rammenta inside (see Fig. 9). *Central column* at apex widened into a disk, often with processes, below this narrowed into the neck and at the base widened and surrounded by the 'annulus interior' above a sulcus, the base of the flower tube often thickened into an 'annulus exterior' which can be almost or totally obsolete. *Anthers* with one apical pore, sessile, situated around the overhanging rim of the column. *Ovary* 1-locular with many placentas. *Fruit* berry-like. *Seeds* thick-walled, c. 1 mm long and with a shorter appendage. — **Fig. 6–9, Plates 1–4.**

Distribution — About 13 species from the Kra Isthmus of Thailand through *West Malesia*, including Luzon and Mindanao in the Philippines. Possibly formerly also in Bali.

Habitat — In primary and secondary forest, the host *Tetrastigma* species prefer to grow in rich alluvial or limestone derived soils. As a result they never occur in areas with *Gleichenia* thickets. Moreover they are restricted to altitudes below about 2000 m. The highest reported *Rafflesia* is the site on Mt Leuser where Van Steenis found *R. rochussenii* at 1800 m. Most of the known localities are around 1000 m or lower. That may be the reason *Rafflesia* is now very rare on the rather denuded lower mountain slopes of West Java.

Some of the best *Rafflesia* and *Rhizanthes* sites are found outside old primary forests since *Tetrastigma* species germinate best in open disturbed soils from the seeds dispersed by birds or small mammals. How well the parasites can survive in severely cut back climbers is still unknown, but this can now be checked at some sites where silvicultural operations have damaged populations.

Ecology — Always parasitic on the trailing stems and/or roots of some species of *Tetrastigma* (Vitaceae).



Fig. 8. *Rafflesia*. Fully open flowers. For each species a flower of average size is pictured from above. a: *R. manillana*, b: *R. rochussenii*, c: *R. tengku-adlinii*, d: *R. cantleyi*, e: *R. pricei*, f: *R. kerrii*, g: *R. hasseltii*, h: *R. gadutensis*, i: *R. patma*, j: *R. tuan-mudae*, k: *R. micropylora*, l: *R. keithii*, m: *R. schadenbergiana*, n: *R. arnoldii*. Drawn by Janis Atlee, from different sources in archives W. Meijer (MO).

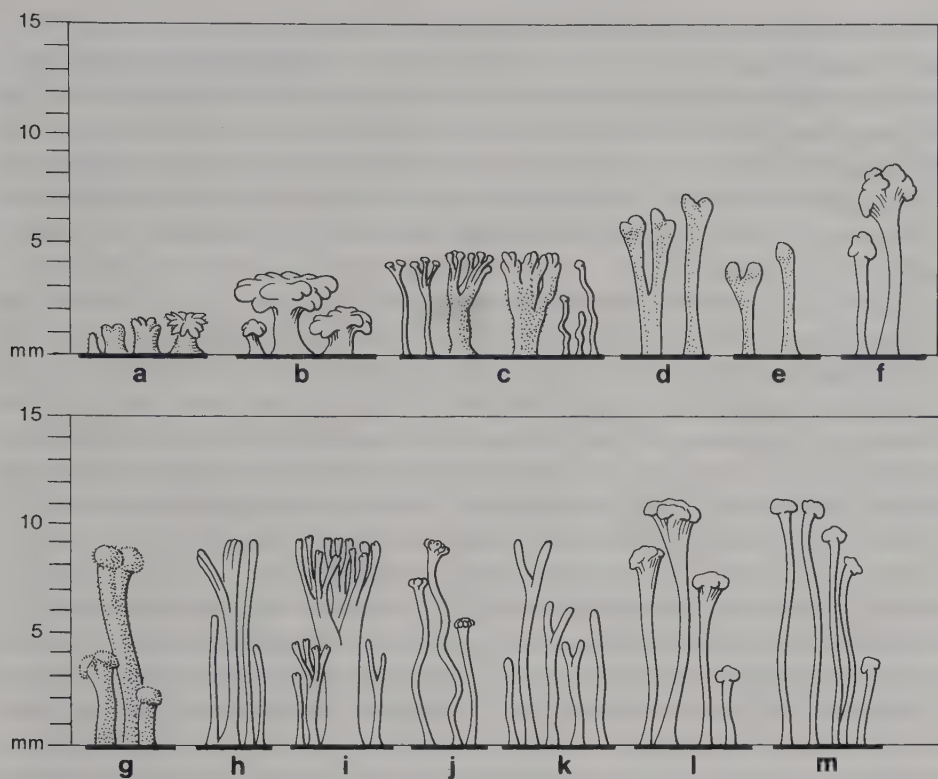


Fig. 9. *Rafflesia*. Ramenta from inside of perigone tube from 13 species, drawn on scale. a: *R. patma*, b: *R. manillana*, c: *R. tengku-adlinii*, d: *R. pricei*, e: *R. keithii*, f: *R. gadutensis*, g: *R. micropylora*, h: *R. kerrii*, i: *R. arnoldii*, j: *R. rochussenii*, k: *R. schadenbergiana*, l: *R. cantleyi*, m: *R. hasseltii*. Drawn by Janis Atlee, from different photographs in archives W. Meijer (MO).

Taxonomy — Winkler [Planta 4 (1927) 1–97] suggested a subdivision based on the structure of ramenta, which appear to have great diagnostic value in tracing the possible phylogeny of species in this genus. Comparative research of the ribosomal RNA of surviving species can test this assumption.

Historical review — The first botanical explorer who found *Rafflesia* in Malesia was the prominent but ill-fated French surgeon-naturalist Louis Auguste Deschamps. He sailed from 1791 to 1794 during the great upheavals of the French revolution with the expedition of the 'La Recherche' in search of the lost research ship 'La Pérouse' (Van Steenis-Kruseman 1950; Van Steenis et al. 1954). In March 1794 the ships, after giving up the search, were in the harbour of Surabaya in East Java and the commander of the expedition refused to proceed in view of the situation in France. Deschamps and his companions let themselves be interned by the Dutch colonial authorities. Deschamps, who apparently showed great interest in the local language, people, flora and fauna was

invited by Governor Van Overstraten to make natural history studies all over Java for three years, making with the help of special assistants many notes, drawings and collections and even starting on a manuscript entitled 'Materials towards a Flora of Java'. That still marvelous island must during that time have been for him a botanical paradise. In 1798 he could return with his treasures to France but meanwhile the British were at war with the French and blockaded France from the sea. The ship on which Deschamps sailed was taken by the British and all the specimens and notes of Deschamps were confiscated.

Years later the manuscripts and some specimens turned up at a public sale at the Indian House in London and were bought by John Reeves, who donated them in 1861 to the British Museum (Natural History). The specimens were never seen again (Van Steenis-Kruseman 1950). It lasted until about 1954 when the manuscripts could be studied by C.A. Backer, Mrs and Prof. van Steenis, who to their surprise discovered that among these notes were sketches of buds and host plants of *Rafflesia*, most likely seen by Deschamps on Java, long before the well-known so-called first discovery of what somebody called that stupendous plant (Mabberley) by Arnold and Raffles in the southern part of Bengkulu (Benkoelen, Bencoolen) in Sumatra in 1818. There are suspicions by Mabberley and Van Steenis (unpubl. letters) that British botanists possibly knew that Deschamps had found a very strange plant and that there was a kind of secret competition going on to see who would first unravel further this wonder of nature. That might have been one of the reasons why the young and eager botanical explorer-surgeon-naturalist William Jack, replacing Arnold who died of malaria soon after he did his discovery, rushed at the instructions of Raffles a description of *Rafflesia* as *R. titan* Jack, already forwarded to Marsden by Raffles in April 1820, into print in August 1820 [see W.J. Hooker (1835) 135, 136] in an Appendix of his Malayan Miscellanies at the Missionary Press in Bengkulu. Actual publication of this Appendix was kept back while the Linnean Society took long to print the paper on *R. arnoldii* R.Br., read by Brown on 30 June 1820 at the meeting of this prestigious society. Whoever got the name first published it should be a British botanist. (See also page 35 under the Incompletely known species.) Rivalry between the British, French and Dutch was great at that time.

The supposition of Merrill (1952) that the names *R. arnoldii* and *R. titan* were based on the same types is wrong. Jack collected plenty of extra materials for Brown and himself after Raffles had forwarded letters and specimens to Sir Joseph Banks, who delegated the description to Brown (Mabberley 1985) and he also established for sure that the plant was a parasite on a kind of grapevine, later called the genus *Tetrastigma*. Soon after Jack had assured Robert Brown that his publication was only a kind of backup action he died of a lung disease and only a few copies of his Appendix had been sent by him to Wallich in Calcutta and to Brown, while the main shipment went into flames at sea not far from the harbour of Bengkulu with all of Raffles's belongings on his way back to England. Raffles managed to get ashore again and started a recollecting drive (Mabberley 1985). See also details on Jack in Hook. Comp. Bot. Mag. 1 (1835) 121–147. He was a marvelous very promising botanist like Arnold and later Kuhl and Van Hasselt who were less lucky than Deschamps to get out of malaria-infested Java alive.

Just a few years after Brown received letters from Jack about the fruits of *Rafflesia* and its host specificity another *Rafflesia* event unfolded in Java where since 1818 the very young and ambitious (only 22 years old in 1818) German-Dutch surgeon-naturalist C.L. Blume was stationed as inspector of vaccines and in 1822 as Director of the Buitenzorg (now Bogor) Botanical Garden. He used the fortune of his rich first wife to launch large expeditions in the wilds of Java, during one of which he found out about a large bud and some kind of flower in the Nusa Kambangan Peninsula along the southcoast of Java. He succeeded to find it, first did not recognize it as a flowering plant, but soon compared it with the excellent illustrations of the Bauer brothers who worked for Robert Brown. By the time he had returned to Holland the German plant collector A. Zippelius had found on Mount Salak near Bogor what appeared to be a second genus related to *Rafflesia*. Blume described his new *Rafflesia patma* and also the new genus and species which he named *Brugmansia zippelii*, unfortunately using a genus name already occupied in *Solanaceae*. In beauty and interesting flower biology this genus, now known as *Rhizanthus*, equals *Rafflesia* and the large plates and long descriptions in *Flora Javae* by Blume are very impressive although difficult to read in his elaborate Latin prose (Backer 1921).

Subsequently other discoveries were made: the very small *Rafflesia manillana* in Luzon (Teschemacher 1841); in 1850 a rather small novel *Rafflesia* species with a completely unarmed disk of the central column, collected by an unknown plant collector of the Bogor garden on the Gedeh-Pangerango outlayers near Cibodas and described by Teijsmann & Binnendijk (1850) as *R. rochussenii*. In 1884 *Rafflesia tuan-mudae* was found by O. Beccari in Sarawak. The Central Sumatra expedition of D.D. Veth in 1884 had the very distinct *R. hasseltii* as one of its main trophies. It was recently rediscovered by the French botanist-cartographer Yves Laumonier and by Harry Wiriadinata from Bogor.

Solms-Laubach (1891) commented on the two species known from the Philippines and he described in 1910 *R. cantleyi* from Malaya.

Meanwhile the few known localities of *Rafflesiaceae* within easy access from Bogor had been mined out so much for all sorts of anatomical-morphological research and attempts to transplant the parasites wholesale attached to the hosts to the Bogor Botanic Garden, that the original localities became depleted.

Koorders (1918) described a number of new species from collections by Witkamp and others; Meijer (1984) added five and Mat Salleh & Latiff (1989) one. In 1992 *R. kerrii* was found back in the Malay Peninsula (Wong 1993).

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Ex situ cultivation — There are reports by Teijsmann (1850) and J.J. Smith (1929) about transplantations of *Tetrastigma* with *Rafflesia* from their natural sites to the Bogor Garden. In 1850 H.H. Loudon from Nusa Kambangan assisted with the transfer of *Rafflesia patma* [see a letter from Teijsmann to De Vriese, dated 23 July 1852 in De Vriese (1853)]. This plant flowered from 23 until 25 March 1850 and again the 6th of October. Docters van Leeuwen (1929) cited the same flowering dates and this proves that in fact *R. patma* was not grown from seeds as he asserted. *Rafflesia rochussenii* was added to the garden collection from transplants after 29 July 1850 (Teijsmann & Binnendijk 1850). By 1856 *Rafflesia arnoldii* had been added to it (see Teijsmann 1856a; Teijsmann & Binnendijk 1866).

According to a short note in *Botanische Zeitung* of 15 May 1857 (p. 328), the Dutch newspaper *Haarlemsche Courant* of 7 April 1857 stated (translated): "*Rafflesia arnoldii* flowered on 9 February 1857 in the Botanic Garden of Buitenzorg, Java. This flower came from a plant which grew as the result of Teijsmann's attempts to inoculate a wild grape vine. The flower was immediately illustrated at the spot." Most likely this is the one figured by Miquel (1863).

As mentioned above, Teijsmann (1856a, b) reported in several papers about his inoculation experiment, also in a French version (Teijsmann 1858). Binnendijk, in a letter to Motley (Motley 1857), claimed that he in fact did the actual inoculation which took place in November 1854. The first buds were visible in August 1855 and as we saw the first flower appeared February 1857.

Seeds were said to have been taken from a fruit grown in the garden but it is rather obscure how the flower which produced that fruit was pollinated. Also the subsequent history as reported by Solms (1875) and Beccari (1875), suggesting that this plant was bisexual, self-pollinating or parthenocarpic is very confusing as already explained above. It shows that careful documentation and labelling in situ and good record keeping is absolutely needed in such experiments.

In 1866, there were three species of *Rafflesia* (*R. patma*, *R. arnoldii* and *R. rochussenii*) at the Bogor Garden according to the Garden Catalogue (Teijsmann & Binnendijk 1866). Docters van Leeuwen (1929) cited old mantri Noerkas as remembering a flower in 1879.

The situation in 1883/84 was described by Solms (1891). Beccari (1875) reported to have seen flowers of *R. patma* in Bogor when he visited the Gardens between 30 January and 2 February 1872.

Beccari saw *R. arnoldii* in the Bogor Garden in 1874 (Beccari 1875) and reported that the species flowered every year. Reports from Docters van Leeuwen can be projected back in time around 1889 and around 1898 according to J.J. Smith (1929). Raciborski made according to Smith new attempts to transplant *R. patma* from Nusa Kambangan. The last year *R. rochussenii* and *R. patma* flowered in Bogor was 1929 (Docters van Leeuwen 1929; J.J. Smith 1929). Since 1929 no further attempts were made by anybody connected with the garden since localities were depleted, partly due to over-collecting or totally destroyed by land cultivation or protected in tiny nature reserves (see also Brewer 1918).

Docters van Leeuwen wrote in a Dutch article (1929) that his horticulturist P. Dakkus repeated a seed inoculation experiment in August 1924 with seeds of *Rafflesia rochussenii* from a fruit supplied by Ader from Mt Garut. This was done in the Fern-Bromeliad Garden on stems of *Tetragium lanceolarium* (now *T. leucostaphylum*). In January of 1929, 4.5 years later, a flower appeared as a result of this. Dr. Frits Went made photographs of it.

Rafflesia rochussenii seems to be the only species of the genus that has ever flowered in a greenhouse in the temperate zone. De Vriese (1853) illustrated this species from a plant grown in the Leiden Botanical Garden. The infected host plant must have been transported in a wardian case by ship all the way from Java. I have not been able to find any special report about the actual flowering date in a local newspaper of that time nor a reference in *Botanische Zeitung*.

References: Beccari, O., *Nuovo Giorn. Bot. Ital.* 7 (1875) 70–75. — Brewer, F.W.J., *Meded. Natuurmon. Ned.-Indië* nr. 2 (1918) 19–21. — Docters van Leeuwen, W.J., *Trop. Natuur* 18 (1929) 43–45. — Miquel, F.A.W., *Choix des plantes rares ou nouvelles cultivées et dessinées dans le Jardin Botanique de Buitenzorg* (1863) pl. 1. — Motley, J., Extract from a letter. *Hook. J. Bot. & Kew Gard. Misc.* 9 (1857) 148–153. — Smith, J.J., *Trop. Natuur* 18 (1929) 156. — Solms-Laubach, H., *Abh. Naturf. Ges. Halle* 13, 3 (1875) 40 pp., t. 24–27; *Ann. Jard. Bot. Buitenzorg* 9 (1891) 184–246. — Teijsmann, J.E., *Nat. Tijds. Ned. Indië* 1 (1850) 431–440; *ibid.* 12 (1856a) 279–281; *Hook. J. Bot. & Kew Gard. Misc.* 8 (1856b) 371–374; *Ann. Hort. Bot., Fl. Jard. Roy. Pays-Bas* (1858) 27–30. — Teijsmann, J.E. & S. Binnendijk, *Nat. Tijds. Ned. Indië* 1 (1850) 425–430; *Cat. Plant. Hort. Bot. Bogor.* (1866) 15. — Vriese, W.H. de, *Mémoire sur R. rochussenii et patma* (1853) 9 pp., 2 pl.

KEY TO THE SPECIES AND VARIETIES

- 1a. Ramenta short, more or less pustulate, only a few millimetres long, in some cases clavate 2
- b. Ramenta more than 2.5 mm long 4
- 2a. Flowers 15–20 cm in diam. Opening of diaphragm (orifice) relatively wide, leaving the lower inner side of the flower tube exposed to view from above. Anthers c. 15 **7. *R. manillana***
- b. Flowers at least 25 cm in diam. Orifice of diaphragm too small to expose the inner side of the flower tube. Anthers 20–40 3
- 3a. Flowers (15–)30–60 cm in diam. Rim of disk steeply raised. Anthers (25–)32–40. Ramenta very short knobs **9. *R. patma***
- b. Flowers 26–30 cm diam. Disk rim only slightly raised. Anthers about 20 See *R. borneensis*, under Incompletely known species, p. 34
- 4a. Perigone lobes and diaphragm in general red or orange throughout, including the warts. Diameter of flowers on average 20 cm (15–30). Ramenta slender and swollen at apex 5
- b. Perigone lobes with white warty blots, or disk with many processes, or flowers larger than 30 cm diam. (*R. micropylora*) 6
- 5a. Disk of flowers totally smooth or with up to 8 processes, rim not raised. Anthers 15–20 **11. *R. rochussenii***
- b. Disk with c. 25 processes, rim raised. Anthers 20 **13. *R. tengku-adlinii***

- 6a. Orifice of diaphragm angular or slightly lobed, very small compared to the size of the flower, 3–9 cm in diam., too small to be able to count the c. 15 processes. Ramenta often branched and apices of branches globular, swollen. Flowers 30–60 cm diam. Warts on perigone lobes reddish **8. *R. micropylora***
- b. Diaphragm opening relatively larger 7
- 7a. Apices of the ramenta either more or less distinctly swollen or crateriform ... 8
- b. Apices of the ramenta not distinctly swollen 10
- 8a. White warts across the base of the perigone lobes very large, 4 or 5 only. Ramenta slender, apices swollen. Anthers c. 20. Diaphragm with only one basal ring of dark-brown warts **4. *R. hasseltii***
- b. White warts across the base of the perigone lobes more than 5. Diaphragm with several concentric rings of warts 9
- 9a. White warts across the base of the perigone lobes 10–12. Some ramenta with swollen, others with crateriform apices. Anthers c. 30 **3. *R. gadutensis***
- b. White warts across the base of the perigone lobes 7–9. Ramenta slender, all with swollen apices. Anthers 20–25 **2. *R. cantleyi***
- 10a. White warts in tangential direction about halfway along the perigone lobes relatively covering less space than the red parts, c. 8 in number
..... See *R. tuan-mudae*, under Incompletely known species (p. 36)
- b. White warts on perigone lobes more numerous 11
- 11a. Flowers c. 70 cm in diam. White warts on the perigone lobes very small, covering far less space than the red-coloured part. Anthers (20?–)24–30
..... **6. *R. kerrii***
- b. White warts on the perigone lobes covering more space than the red-coloured part 12
- 12a. White warts across the base of the perigone lobes 5 or 6(–10) 13
- b. White warts across the base of the perigone lobes more than 10 14
- 13a. Flowers up to 80 cm diam. Lower face of the diaphragm with ramenta. Anthers 26–38 **12. *R. schadenbergiana***
- b. Flowers (16–)25–37.5 cm diam. Lower face of diaphragm without ramenta. Anthers c. 20 **10. *R. pricei***
- 14a. Larger white blots on perigone lobes interspaced with numerous small ones. Circular blots on diaphragm contrasting, isolated and with broad dark-brown margin **5. *R. keithii***
- b. Larger white blots on perigone lobes not or very sparsely interspaced with smaller ones. Circular white blots on the diaphragm little contrasting with their surrounding tissues, often more or less connected in a network of dark reddish bands and with only a thin dark reddish margin 15
- 15a. Ramenta covering the inner side of the flower tube from the rim of the diaphragm downwards to the outer annulus **1a. *R. arnoldii* var. *arnoldii***
- b. Ramenta missing in a zone above the outer annulus at the base of the column ...
..... **1b. *R. arnoldii* var. *atjehensis***

1. *Rafflesia arnoldii* R.Br.

Rafflesia arnoldii R.Br., Trans. Linn. Soc. 13 (1821) 201; 19 (1845) 221, t. 22–26; Solms-Laubach, Ann. Jard. Bot. Buitenzorg 9 (1891) 237, t. 27, 28; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 31, pl. 1, 2, 3; Coomans de Ruiter, Trop. Natuur 22 (1933) 165; 188 (as *R. tuan-mudae*); Meijer, Nat. Geogr. 168 (1984) 136. — Type: *Raffles & Arnold s.n.* (K).

a. var. *arnoldii*

Mature *buds* up to 30 cm diam. *Flowers* (55–)70–100 cm in diam. *Perigone lobes* with up to c. 15 white warts in radial and lateral direction, only occasionally interspersed with smaller white warts, the white warts occupying slightly more space than the reddish brown background. Processes on the disk (20–)35–40(–50). *Diaphragm* with an opening about 2/3 of the total diaphragm diameter, raised rather high at the end of flowering phase, upper face light reddish pink with c. 40 radial series of 4 or 5 white circular warts which are only a few mm in diameter, lower face just below the rim with 3 or 4 series of white rounded blots. *Ramenta* up to 10 mm long when mature, all over the inner side of the flower tube, simple or forked and when fresh with papillose fluffy apices, never crateriform swollen like in *R. gadutensis*. *Male flowers* with 36–40 anthers.

Distribution — *Malesia*: Sumatra (Aceh, W Sumatra, Bengkulu, Lampung), Borneo (W Sarawak, W Kalimantan).

Habitat — Primary and disturbed lower montane forests, up to c. 1000 m altitude.

Ecology — Host plant most commonly *Tetrastigma leucostaphylum* (Dennst.) Alston ex Mabb. [= *T. lanceolarium* (Roxb.) Planch.].

Notes — 1. See also under Incompletely known species, *Rafflesia tuan-mudae* Becc., p. 36.

2. A plant of this species flowered on 9 February 1857 in the Bogor Botanical Garden. See paragraph on ex situ cultivation, p. 20.

b. var. *atjehensis* (Koord.) Meijer

Rafflesia arnoldii R.Br. var. *atjehensis* (Koord.) Meijer, comb. et stat. nōv. — *Rafflesia atjehensis* Koord., Bot. Overz. Raffles. Ned.-Indië, Nieuwe Addenda (1918) 11; Bull. Jard. Bot. Buitenzorg 3 (1918) 77, 3 pl. — Type: *Koorders 44060* (BO).

This variety differs only in the almost glabrous, 2 cm wide zone at the base of the perigone tube, with only scattered, very short (3–6 mm long) ramenta.

Distribution — So far only known from the type locality Aceh, Locop. Possibly also near Bohorok near the boundary of the Leuser National Park.

Habitat — Lowland Dipterocarp forest.

2. *Rafflesia cantleyi* Solms-Laubach

Rafflesia cantleyi Solms-Laubach, Ann. Jard. Bot. Buitenzorg, Suppl. 3 (1910) 1. — Type: *Cantley s.n.*, received at Kew in 1887, fragments given to Solms in 1901, seen by the author in STR.

Rafflesia hasseltii auct. non Suringar: Meijer, Mal. Naturalist 36 (1983) 21, 2 col. photos, map; Wong, Nature Malays. 15 (1990) 56–59, col. photos.

Flowers c. 30–55 cm across, in all respects very much like *R. hasseltii* but *perigone lobes* with about 6–8 big whitish warts in radial and lateral direction and up to 10 in the basal rows, sometimes these blots more or less confluent in bizarre wavy edged configurations. *Diaphragm* opening rounded or angular, almost half as wide as the total diameter, 4–8 cm broad upper face light pinkish or whitish with about 25 radial series of 3 or 4 dark red circled dots; lower face above the insertion with 3 concentric series of stalked toadstool-like ramenta, with 5 mm long stalks and capped by 5–8 mm wide disks, towards the rim 5 concentric series of oval white blots, 12–15 mm wide and 8–10 mm in radial direction. *Ramenta* covering the inner face of the *flower tube* 10–12 mm long, partly branched, with swollen apices, papillose grainy, lower down shorter, c. 2 mm long. *Male flowers* with 20–25 anthers.

Distribution — *Malesia*: Malaya (Perak, Kelantan, Pahang, Tioman I., Kedah), see map in Meijer, l.c. 1983, updated (in ms) by Matthew Wong. See also Meijer & Wong, Mal. Naturalist 47 (1993) 10–11.

Habitat — Lowland Dipterocarp forest and secondary forest.

Notes — 1. This species was up to 1984 considered by the author to be identical with *R. hasseltii* Suringar, following identification by Ridley and others.

2. See also note 2 under *R. hasseltii*.

3. *Rafflesia gadutensis* Meijer

Rafflesia gadutensis Meijer, Blumea 30 (1984) 211; Weevers in Koningsberger (ed.), Leerb. Alg. Plantk. 2 (1942) f. 186 (as *R. arnoldii*); Richards, Trop. Rain Forest, ed. 2 (1996) 155: f. 6.23; Meijer, Pal-mengarten 60/2 (1997, '1996') 38–41. — Type: *Meijer 17003* (BO holo; MO), W Sumatra. *Rafflesia spec.*: Schaefer, Trop. Natuur (1940) 21–23;

Flowers 40–46 cm diam. *Perigone lobes* with 10–12 whitish-pinkish blots along the median and along the base, largest blots 2 by 1 cm, few small blots in between, some of the larger sometimes merged and up to 5 cm broad. *Diaphragm* opening about 2/3 of the total width, pinkish red with about 30 radial rows of circular light pinkish red margined warts, lower face of diaphragm with 5 concentric rings of white blots close to the rim, the two rings of warts closest to the perigone tube with flat or somewhat crateriform oval fringed apex, c. 9 by 8 mm across, the tops supported by 1–2(–6) mm long stalks, making them look like minuscule toadstools. *Perigone tube* c. 8 cm deep, covered at the inside with rather fugaceous ramenta which are 6–8(–9) mm long and have swollen heads 1 mm long and 2–3 mm wide, sometimes crateriform at apex, stalks c. 1 mm across, a few branched or lobed ones near the diaphragm. Between the ramenta on the inner side of the perigone tube some scattered toadstool-like protuberances close to the inside of the diaphragm, but with only 1–2 mm long stalks. *Male flowers* with c. 30 anthers. — **Plate 1.**

Distribution — *Malesia*: W Sumatra (Westcoast, Ophir District, Padang–Bukittinggi; Bengkulu, Kayu Tanam, Padang–Solok, Ulu Gadut).

Habitat — Primary and secondary lower montane forest, around 350–600 m altitude.

Notes — 1. First seen by Korthals around 1834 and illustrated for him but unpublished; also copies made for Solms-Laubach. Also found near the gold and silver mine Simau, Bengkulu, and photographed there around 1934 by K. Schaefer [see Schaefer, *Trop. Natuur* 29 (1940) 21–23].

2. Beccari collected the species in August 1878 near Ayer Mancior, the waterfall in the Anei Canyon between Padang and Bukit Tinggi, at about 360 m altitude near Kayu Tanam, West Sumatra. He and Solms-Laubach misidentified this species as *Rafflesia arnoldii*.

4. *Rafflesia hasseltii* Suringar

Rafflesia hasseltii Suringar, Acta Soc. Reg. Sc. Neerl. 25 Oct. 1879 (1880?) [4–5]; Assoc. Avanc. Sciences, Congr. Alger (1881) 621–626, pl. 11, 12; in Veth, Midden-Sumatra (1884) 13, t. 1, 2; Solms-Laubach, Ann. Jard. Bot. Buitenzorg 9 (1891) 23; in Engl., Pflanzenz. 5 (1901) 9, f. 1; Ann. Jard. Bot. Buitenzorg 3, Suppl. pt 1 (1910) 1–4, pl. 1–6; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 76–81, pl. 12; Theunissen, Trop. Natuur 13 (1924) 150–152, 2 f.; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 264; Meijer, Grasduinen 5 (1991) 65, photo. — Type: *Suringar* (L).

Flowers c. 38–50 cm diam. *Perigone lobes* c. 11.5–13 cm long and 15–17 cm wide, with about 5 large pustules across, these ranging from 5 by 3 to 10 by 1 cm. *Perigone tube* c. 18–20 cm wide, neck of column 3 cm. Processes 15–24, coloured like the disk, light yellowish, but dark brown at the apex and not flattened as in some other species. *Diaphragm* opening about half as wide as apex of flower tube, pale whitish or yellowish with a dark brown zone near the rim and a basal ring of rounded or oblong dark brown warts. Upper zone of the flower tube near attachment of the diaphragm with 4 rings of toadstool-like compound *ramenta*, grading into white blots at the lower face of the diaphragm. Numerous bristles on lower face of the corona (= crest of the disk) and all along the column. *Ramenta* linear, with swollen apices. *Male flowers* with 20 anthers.

Distribution — *Malesia*: Sumatra (W Sumatra, Riau, Jambi), Peninsular Malaysia.

Habitat — Primary and secondary lower montane forest, around 400–600 m altitude.

Notes — 1. Of the six localities known four were located during the last 10 years.

2. This species is closely related to *Rafflesia cantleyi* and seems to hybridize with it in the Malay Peninsula.

3. The description was composed from the original one and from a few fragments of the type in L and some photographs. Most records come from pictures.

5. *Rafflesia keithii* Meijer

Rafflesia keithii Meijer, Blumea 30 (1984) 211; Salleh & Latiff, Blumea 34 (1989) 113. — Type: *Madani s.n.* (SAN holo, in spirit), Sabah, Sungai Melaut.

Rafflesia spec.: Corner in Luping et al., Kinabalu, summit of Borneo. Sabah Soc. Monogr. (1978) 136, 168, t. 154, photos.

Mature *buds* up to 25 cm diam. *Flowers* on average c. 80(–94) cm in diameter (few records). *Perigone lobes* with rather dense numerous white warts, small ones interspers-

ed with larger ones, the latter about 10–12 across the greatest breadth of the lobes. *Diaphragm* with 5 concentric rings of white warts in about 40 radial rows, each surrounded by a dark red brown margin, lower face of diaphragm with 5 or 6 rings of white blots, those of the ring closest to the opening for a large part confluent, towards the transition into the flower tube not with ramantae formed like white-headed toadstools (stalked disks), but uniformly with the same type of long ramantae as those on the inner side of the flower tube. *Perigone tube* densely covered with ramanta inside, the ramanta 5–6 mm long near the diaphragm and often fascicled (in bundles), only a few branched. Disk 11–13.5 cm in diam. Processes 38–42(–46), flattened. Annulus interior in a bud of 22 cm diam., 2 mm wide, annulus exterior flat, 5 mm wide and grooved. *Male flowers* with about 40 anthers and with dense bristles on the lower face of the crest of the disk and around the anther cavities. *Female flowers* with a swollen ring along the lower rim of the crest of the disk, c. 3 mm high and broad. — **Plate 2.**

Distribution — *Malesia*: Borneo (Sabah, most likely also in E Kalimantan, see *R. witkampii* under Incompletely known species, p. 36).

Habitat — Upper Dipterocarp forest with *Parashorea malaanonan*, around 500–600 m altitude.

Ecology — Host plant *Tetrastigma leucostaphylum* (Dennst.) Alston ex Mabb., very possibly also *T. diepenhorstii* Miq. (= *T. trifoliolatum* Merr.) but proof only from the former with a host plant with very low branches.

Notes — 1. At first sight this taxon comes close to *R. arnoldii* as defined in this revision. However, close study of the ramanta reveals that the single, toadstool-shaped ones that are typical for *arnoldii* are missing in *keithii* (and in *pricei*, possibly the nearest relative of *keithii*). This view is supported by the occurrence of a hybrid at the Mamut copper mine *Rafflesia* sanctuary in Sabah (Jamili Nais, oral comm.).

2. A main problem is still the lack of good documentation and sharp colour photographs of *Rafflesia* specimens with mature flowers from E Kalimantan.

6. *Rafflesia kerrii* Meijer

Rafflesia kerrii Meijer, Blumea 30 (1984) 212; Meijer & Elliott, Nat. Hist. Bull. Siam Soc. 38 (1990) 117–133. — Type: *Kerr 16980* (K holo; BM), Phuket.

Flowers up to 70 cm diam. *Perigone lobes* up to c. 20 cm long and 24 cm wide, with scattered rather numerous warts, with 3–4 mm space between them, the warts smallest relative to the red background of any species known. *Perigone tube* with ramanta which are mostly unbranched and only slightly swollen at apex, those near the diaphragm c. 10 mm long, those near the base of the tube 5 mm. *Diaphragm* only slightly lighter red than the perigone lobes, about 30 cm in diameter with a central opening about 20 cm across; upper face with about 3 to 4 concentric rings of circular whitish, dark red ringed spots, in about 30 radial lines; lower face with 7 concentric rings of white blots, which are up to 7 mm across. Central part of disk with 32–40 flattened processes, 2–2.5 cm long. *Male flowers* with 25–30 anthers.

Distribution — Peninsular Thailand; *Malesia*: Peninsular Malaysia (Kelantan: Bukit Tepoh; Kelantan-Perak border: Mt Chamag; Perak: Bintang Range).

Habitat — Lowland and hill Dipterocarp forests, 500–1000 m altitude.

7. *Rafflesia manillana* Teschemacher

Rafflesia manillana Teschemacher, Boston J. Nat. Hist. 4 (1841) 63, t. 6; Ann. Mag. Nat. Hist. 9 (1842) 381; Solms-Laubach, Ann. Jard. Bot. Buitenzorg 9 (1891) 241, t. 26, f. 7–10; W.H. Br., Philipp. J. Sc., Bot. 7 (1912) 209, t. 12, 21; Merr., Spec. Blanc. (1918) 135; Enum. Philipp. Flow. Pl. 2 (1923) 120; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 264; Pancho, Vasc. Fl. Mt Makiling (1983) 312, f. 98. — Type: *Navarro* specimen from Leyte (A, lost).

Rafflesia philippensis Blanco, Fl. Filip., ed. 2 (1845) 565. — Type: *Navarro* specimen from Laguna, Luzon, now lost.

Rafflesia lagascae Blanco, Fl. Filip., ed. 3, 3 (1879) 231; most likely a nomen nudum.

Rafflesia cumingii R.Br., Trans. Linn. Soc. 19 (1845) 243. — Type: *Cuming* collection (BM), most likely from the same site on Leyte as the *Navarro* collection seen by Teschemacher.

Flower buds up to 8 cm across, cupule 2.5–3 cm high, 4–6 cm wide, bud scales up to 5.5–7 cm long. *Flowers* 15–20 cm wide and 7–9 cm high when expanded. *Perigone lobes* light reddish brown, 4–6 cm long and 5–7 cm wide, white warts a mixture of larger circular with oval ones, about 10–12 along a transverse line halfway the lobes, mixed with numerous white dots. *Diaphragm* c. 1–1.4 cm broad, c. 7 cm in diameter, strongly curved inwards along the opening, which is about 5/6th as wide as the apex of the perigone tube; upper face rather densely randomly covered with oblongish white warts. *Disk* of column c. 2 cm above the base of the perianth tube, 3.2–4.5 cm in diameter including the rim, exposed while the flower is opened; rim of disk with a 3–5 mm high raised part. *Processes* about 14–20(–30), sometimes almost missing in the centre of the disk, 3.5–5.5 mm long, apex cylindric, with bushy cilia. *Neck of column* 1.3–1.8 cm diameter, narrower in male flowers. One prominent annulus, 3 mm broad, 30–38 mm diameter around the base of the column. *Perigone tube* c. 2.5 cm deep, 5 cm wide; ramenta at the inner side in about 12 rows, little stalked outgrowths, 0.5–1 mm high, multilobed at apex, virtually absent near the base of the perianth tube, close to the annulus; in a 1 cm wide zone below the diaphragm with short, warty lobed, whitish, 2–3 mm wide warts. *Male flowers* with 10–15 anthers, relatively large for such small flowers, not hidden in a sulcus as in the larger-flowered species, but attached rather close to the lower margin of the disk; corresponding with each anther in the central column a deep groove which runs down below the anther to the column base. *Female flowers* with ovary 2.5 cm wide at apex, 1.0 cm high, above the annulus without grooves or with very faint ones, less room under the corona (overhang) of the disk than in male flowers, on its lower side a papillose stigmatic zone.

Distribution — *Malesia*: Philippines (Luzon, Samar, Leyte). Most of these records are old history. The species is now rare and endangered.

Habitat — Lowland and hill forests, up to about 1000 m altitude.

Note — This is the smallest known *Rafflesia*, with flowers only about 15–20 cm in diameter, a very narrow diaphragm, the whitish lobed ramenta only up to 1 mm tall and male flowers only with 10–15 anthers.



Plate 1. *Rafflesia gadutensis* Meijer. Sumatra, Ulu Gadut near Padang. Photo W. Meijer, 1983.



Plate 2. *Rafflesia keithii* Meijer. Sabah, Sabah, Mt Kinabalu. Photo Jamili Nais, 1990, donated 1994.



Plate 3. *Rafflesia micropylora* Meijer, Sumatra, Mt Leuser National Park. Photo A. Rijksen.



Plate 4. *Rafflesia pricei* Meijer. Sabah, Tambunan. Photo Julius Kulip, 1989, donated 1992.

8. *Rafflesia micropylora* Meijer

Rafflesia micropylora Meijer, Blumea 30 (1984) 213. — Type: Koorders 44211 (*Badings s.n.*) (BO holotype), Lokop.

Rafflesia cf. *atjehense* auct. non Koorders: W.J. de Wilde, WOTRO-Jaarboek (1972) 38, fig.

Rafflesia spec. 3 and *spec.* 4: Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 109, 111. See note 2.

Flowers 30–60 cm diameter, no data available on size of buds. *Perigone lobes* dark orange-red all over, 16–18 cm long, warts light pinkish, little contrasting with their surroundings, about 10 across at the base, with many smaller warts in between. *Diaphragm* darker red than the perigone lobes, c. 20–25 cm diameter, upper surface with 3–5 concentric circles of circular reddish warts with darker red margins, weakly contrasting, in about 40 radial lines; lower side of diaphragm with about 3(–5?) concentric circles of flat circular knobs, c. 10 mm in diameter, on 5 mm high stalks, grading into the ramenta towards the upper rim of the perigone tube; opening small, c. 3–9 cm wide, sexangular or heptangular, sometimes weakly lobed. *Column* 5–6 cm high, c. 7–8 cm in diameter at the neck. *Disk* 13–14 cm diameter, with about 15 processes. *Ramenta* branched, with swollen apices, c. 12 mm long, those towards the base of the perigone tube only 5–7 mm long and unbranched. *Male flowers* with 40 anthers. — **Fig. 6; Plate 3.**

Distribution — *Malesia*: Sumatra (Aceh). Protected inside the Leuser National Park.

Habitat — In lower montane forests around 300–500 m altitude.

Ecology — Host plant *Tetrastigma leucostaphylum* (Dennst.) Alston ex Mabb., and possibly other species.

Notes — 1. The medium- to large-sized flowers, the small opening of the diaphragm and the richly branched ramenta with swollen apices, make this species easy to recognize.

2. The red-coloured diaphragm, together with the size and the small hole as illustrated in Koorders (l.c.: plate 15, fig. G), make identification of the two numbered species now possible.

9. *Rafflesia patma* Blume

Rafflesia patma Blume, Flora 8 (1825) 609; Flora Javae 1 (1828) 8, t. 1–3; De Vriese, Mém. sur *Rafflesia Rochussenii* et *Patma* (1853); Illustr. *Rafflesia* (1854) t. 5, 6; Rodigas, Fl. Serres 15 (1862–65) 13, t. 1505–1508; Nagelvoort, Nat. Tijds. Ned. Indië 35, VII, 5 (1875) 171–180; Haak, Weekbl. Pharm. 3 (1885) 19 pp., 2 pl.; Observ. *Rafflesia patma* (1889) 4 pl.; Solms-Laubach, Ann. Jard. Bot. Buitenzorg 9 (1891) 238–239, pl. 16, f. 11–16; in Engl., Pflanzenr. 5 (1901) 9, f. 2, 5; Koord., Exk. Fl. Java 2 (1912) 179; Warb., Pflanzenwelt 1 (1913) t. 31, f. D1–5; Hochr., Le Globe 57 (1918) 27–36, photo; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 50–61, pl. 6; Harms in Engl. & Prantl, Nat. Pflanzenfam., ed. 2, 16b (1935) 263; Backer & Bakh. f., Fl. Java 1 (1963) 165. — Type: *Blume* (L), Nusa Kambangan.

Rafflesia zollingeriana Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 67, pl. 10, 11; Backer & Bakh. f., Fl. Java 1 (1963) 165; Ervial, Masters thesis (unpubl.) Agric. College Bogor (1989). — Type: *Koorders 40312* (BO), Java, Puger.

Flower buds prior to expansion up to 21 cm in diameter. Open flowers (30–)37–52 (–60) cm in diameter (in flowers described as *R. zollingeriana* sizes of 20–25 cm re-

ported). *Perigone lobes* flesh-coloured, brown-ocre or carmine red, c. 13–14(–19) cm long and 10–14 cm wide, on the upper face with numerous whitish warts, up to about 25 at the largest breadth, surrounded by much smaller white warts, then same pattern as in *R. keithii*. *Diaphragm* a 5–7 cm wide ring; opening in the centre 5–9 cm across; upper surface strongly pitted, glaucous or with clear circular whitish blots; lower face with 2 series of white oblong-angular blots, two to three times as long tangentially than radially, covered with ramenta or in some cases the region (2–)3–3.5 cm from the margin of the opening and the zone close to the perianth tube devoid of ramenta. *Disk* carmine red, upper face 6–6.5 cm from the bottom of the cupule, (7–)9–13.5 cm in diameter, central part with (24–)37–44(–54) processes 2–3 cm long and 5–8 mm at base, conical or somewhat flattened; corona of the column-disk about 2–2.5 cm high and 1.5 cm wide in radial direction, rim in some cases crenulate, papillose and fimbriate, directed sideways under an angle of about 45°. *Ramenta* reduced to very short (up to 1 mm long) tubercles, some branched. *Male flowers* with about 25–32(–38 in S Sumatra) anthers, 4–6 mm long and across, attached at the inner margin of the corona in a more or less horizontal position, anther cavities 10–15 mm long and 8 mm broad, weakly or not divided by two ridges, partitions between the anther holes provided with cilia. *Female flowers* with a 2–4 mm broad, slightly papillose stigmatic zone divided by a groove; rudimentary anthers c. 1–1.5 mm, in very shallow, broadly triangular cavities. Gully at the neck of the column (sometimes referred to as *Sulcus coronalis disci*) about 8–9.5 cm in diameter, c. 17 mm from the rim of the corona. *Annulus interior* 4–6 mm broad, well defined and sharply elevated (2–3 mm high), or only slightly raised, about 8–9.5 cm in diameter. *Sulcus inter annuli* 3–5 mm wide. *Annulus exterior* 3–10 mm wide average and c. 1 mm thick, rather weakly developed, wrinkled like a rolled-up blanket which is curved into a circle. *Fruit* with cupule 11 cm in diameter, 7–8 cm high, diameter in upper part 7.5 cm, ovarian part 1–2.5 cm high and 5–10 cm wide, side of column with about 40 grooves. Ripe *seeds* 0.8–0.9 mm long, 0.4 mm thick, light-brown to dark-brown.

Distribution — *Malesia*: S Sumatra (Lampung, now extinct?; C and E Java (close to extinction), possibly formerly also in Bali.

Habitat — Most localities are along the south coast of Java in remnants of forest below 400 m altitude.

Ecology — Host species most commonly *Tetrastigma leucostaphylum* (Dennst.) Alston ex Mabb., but possibly also *T. glabratum* (Blume) Planch.

Notes — 1. A medium-sized *Rafflesia*, at first sight much like *R. arnoldii* but the lower side of the diaphragm often covered with ramenta. Warts on the perigone lobes are a mixture of larger and smaller ones, more or less as in *R. keithii* from Borneo. The flower tube is more or less covered with very short knob-like ramenta, not more than one mm long, in some forms partly missing.

2. A form from East Java, with smaller flowers and ramenta almost absent in the lower part of the flower tube, was described by Koorders as *R. zollingeriana*. Ervival (1989) found there in 1989 still viable populations.

10. *Rafflesia pricei* Meijer

Rafflesia pricei Meijer, Blumea 30 (1984) 214; Beaman & J.H. Adam, Sabah Soc. J. 7 (1984) 208–212; Beaman c.s., Amer. J. Bot. 75 (1988) 1148–1162; Mat Salleh, *Rafflesia magnificent* flower of Sabah (1991), several pl.; Meijer, Grasduinen 5 (1991) 63. — Type: *Price s.n.* (K holo), Mt Kinabalu.

Rafflesia schadenbergiana auct. non Goeppert: Meijer, Kosmos 5 (1982) 60, fig.

Rafflesia tuan-mudae auct. non Becc.: Anderson, Bioscience 26, 10 (1976) cover plate; Weber, Sabah Soc. J. 3 (1967) 11, t. 1, 2; Yong, Magnificent Pl. (1981) 2, fig.; Bailes, Kew Mag. 2 (1985) 275, fig.; Jacobs, Trop. Rainforest (1988) 241.

Rafflesia spec.: Dorst, Avant que nature meurt (1965) 153, t. 10; Price, Proc. Cotteswold Nat. Field Club 35 (1968) 93; Morley, Wild Flowers of the World (1970) t. 117C; McKinnon, Borneo (1975) 22, fig.; Bellamy, Botanic Man (1978) 60, fig.; Ayensu, Jungles (1980) 49; Masni, Bt Jubil, Kajian Ekologi dan taksonomi *Rafflesia* di Sabah khususnya di Tambunan, Thesis Univ. Kebangsaan Malaysia (1984); Beaman & J.H. Adam, Sabah Soc. J. 7 (1984) 208.

Mature buds c. 15–20 cm in diameter. *Flowers* (16–)25–30(–45?) cm across. *Perigone lobes* 7–10 cm long and 6.5–14(–19) cm wide, with 10–15 warts at base, many of those wider in the tangential than in the radial direction, some confluent. *Perigone tube* c. 14 cm wide. Column 3–4 cm high, c. 4–5(–9.5?) cm in diameter at the neck. Disk 8.5–9 cm diameter, with 20–40 flattened processes which are about 1–3.5 cm long and up to 1–1.5 cm in diameter. *Diaphragm* (7–)12–13(–17) cm diameter, opening c. 4.5–8.5 cm in diameter, slightly angular and with a white rim surrounded by a dark brown margin; upper face of diaphragm with four concentric rings of warts, those in the third ring from the centre sometimes linear, in the second ring more circular and especially in these two rings surrounded by dark brown margins; lower face of diaphragm with 4 or 5 concentric rings of laterally stretched white bands, without ramenta. *Ramenta* near the diaphragm in fascicled groups, slender, only slightly widened at apex, 2–6 mm long near the insertion of the perigone lobes and 6–7 mm at the base of the tube. *Male flowers* with 20 anthers. — **Plate 4.**

Distribution — *Malesia*: Borneo (Sabah, Sarawak, Brunei, also Kalimantan?). Apparently most populations are on Mt Kinabalu and the Crocker Range and Schwaner Range in Sarawak.

Habitat — Upper Dipterocarp forests with *Shorea platyclados* and lower montane forests, about 400–1300 m altitude.

Ecology — Host species *Tetrastigma leucostaphylum* (Dennst.) Alston ex Mabb.

Notes — 1. This species apparently is now also known from Sarawak (Serian area) and it is possible that a recent discovery of *Rafflesia* by Danna J. Leaman (University of Ottawa) in the Upper Kajan near Long Ampin (East Kalimantan) also belongs to this species.

2. Probably the first collection was made by Joseph and Mary Clemens (nr 28512), on 17 March 1932, near Dallas on Mt Kinabalu. However, we are not quite sure because the specimen does not show the pattern of the warts on the perigone lobes and the size of the flower is almost too large for this species, though the label records “diameter 13–18 inches” (= 32.5–45 cm). Meijer (in Dorst 1965) was the first to publish a photograph of this species on Mt Kinabalu.

11. *Rafflesia rochussenii* Teijsm. & Binn.

Rafflesia rochussenii Teijsm. & Binn., Nat. Tijds. Ned. Indië 1 (1850) 425–430, t. 1, 2; 2 (1851) 651–655; De Vriese, Mém. sur *Rafflesia Rochussenii* et Patma (1853) 4; Illustr. R. Rochussenii (1854) t. 1–3; Solms-Laubach in Engl., Pflanzenr. 5 (1901) 10, f. 6, 7; Ann. Jard. Bot. Buitenzorg, Suppl. 2 (1898) 3–12, t. 1; Ernst & Schmid in Ann. Jard. Bot. Buitenzorg II, 12 (1913) 1–58; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 82, incl. var. *subaculeata* Koord., l.c. 87; Steenis, Trop. Natuur 30 (1941) 179–181. — Type of species and variety: from W Java, lost.

Mature *flower buds* just before opening c. 10–13 cm in diameter. Flowers (15–) 17–20(–30) cm in diam., c. 12 cm high. *Perigone lobes* c. 6.5–8(–9) cm long and 8–9(–11) cm wide, 7–10 cm at insertion. *Diaphragm* c. 11 cm in diam., 2.5–4 cm broad, lower surface covered with short (1–2 mm long) rammenta. *Disk* c. 5.5–6 cm above the base of the cupule, (6–)7–9 cm in diameter, ivory white when fresh, flat or slightly raised in the centre, rim sharp, not raised, centre without processes or with only 1–8 ('var. *subaculeata*'). Sulcus below the disk c. 5 cm in diam. Neck of column 4.5–5.5 cm in diam. *Perigone tube* 12 cm wide in the middle between annulus interior and diaphragm; annulus interior 6.5–7 cm in diam., rather sharp, 2–4 mm thick; annulus exterior a flat 6–8 mm broad zone without rammenta. *Ramenta* long stalked subdiscoïd knobs, c. 10 mm long near the base of the perigone tube. *Male flowers* with 15–20 anthers. *Female flowers* with stigmatic ring distinctly narrowed. *Fruits* c. 8.5 cm wide and 7 cm high, ovary 6 cm wide and 3 cm high, disk decayed, cupula (5–)7–8 cm diam., 1.5–2 cm high.

Distribution — *Malesia*: W Java, N Sumatra (Mt Leuser and further south in Tapanuli). In 1989 and 1990 two sites were rediscovered on Mt Salak, Java, and one around 1995 on Mt Gede, Java (collected by Arindansyah, oral comm. by H. Wiriadinata). The species probably still occurred in Berastagi, Sumatra, in 1980. The site was, however, logged and destroyed in 1981.

Habitat — Lower montane forests up to about 1500 m altitude.

Notes — 1. The most distinctive character is the disk of the column with the rim only slightly raised and the surface bald or only with a few processes, never more than eight. The rammenta are slender and in general have knob-like apices. *

2. Cultivated in the Leiden Botanical Garden in 1851 from dug-up plants (see paragraph on ex situ cultivation, p. 20) and illustrated from damaged flowers by De Vriese in 1853 and 1854.

12. *Rafflesia schadenbergiana* Göpp.

Rafflesia schadenbergiana Göpp. in Hieron., Bull. Internat. Bot. Horticult. St. Petersb. ('1884', 1885) 35–36, 1 pl.; Gartenflora 34 (1885) 3–7, pl. 1177; Ueber *Rafflesia schadenbergiana* Goepp., Ein Beitrag zur Kenntnis der Cytinaceen (1885) 1–10, t. 1, 2; Solms-Laubach, Bot. Zeitung (1885) 507; Ann. Jard. Bot. Buitenzorg 9 (1891) 189. — Type: *Hieronymus s.n.* (K, WRSL iso?).

Flower buds prior to expansion 16–20 cm in diameter, cupule 10–14 cm in diameter, bracts up to 17–18 cm long, 12–13 cm wide. Open *flower* about 80 cm diameter. Rammenta on the inside of the *flower tube* 7–10 mm long, filiform, somewhat thickened at apex, or branched, partly in fascicles. *Diaphragm* 6–8 cm from insertion to opening,

opening 13–14 cm in diameter, margin with pinkish zone, lower face except the marginal zone provided with ramenta c. 4–5 mm long. *Perigone lobes* 25–26 cm diameter, with yellowish whitish warts, which are laterally stretched, irregular shaped, partly connected and about 4 or 5 across in the middle part. *Disk* 12–13 cm diameter, processes 30–50. *Male flowers* with 26–38(–40) anthers.

Distribution — *Malesia*: Philippines (Mt Apo, Mindanao). No records during the 20th century.

13. *Rafflesia tengku-adlinii* Salleh & Latiff

Rafflesia tengku-adlinii Salleh & Latiff, *Blumea* 34 (1989) 111–116; *Fl. Males. Bull.* 11 (1995) 425–428. — Type: *Mat Salleh c.s. KMS 2180* (UKMS holo), Trus Madi Mts.

Mature *flower buds* about 13 cm in diameter. *Flowers* rather small, c. 20–24 cm in diameter. *Disk* about 6 cm diameter and neck of column 3 cm. *Perigone lobes* and *diaphragm* orange throughout including randomly distributed roundish warts, except near the opening, the diaphragm progressively dark reddish towards the centre. *Diaphragm* about 12.5 cm wide, with a 5 cm wide aperture. *Ramenta* slender, 3–5 mm long, partly branched and always with swollen apices, density somewhat reduced towards the opening and at the base of the tube, also present on the lower face of the diaphragm. *Disk* c. 7 cm diameter, flattened processes 25. *Male flowers* with 20 anthers.

Distribution — *Malesia*: Sabah, eastern slopes of Mt Trusmadi. Locality destroyed by loggers a few weeks after the plants were discovered. Later also found in the Gunung Lutong area at 600 m altitude inside the Yayasan Sabah concession.

Most likely the same species as the one seen by Meijer around 1964 near Telupid as a decaying flower.

Note — The measurements of the column, neck and disk were inferred from the drawing with the original description.

INCOMPLETELY KNOWN SPECIES

Rafflesia borneensis Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 47, pl.4. — Type: *Witkamp* collection (BO).

Relatively small *flowers* up to only 20–30 cm in diameter. *Flower tube* very flat and disk of column with a rather flat rim. *Ramenta* as far as seen in the specimen very short and sparse; Koorders described them as very short, rarely longer than 1 mm, with narrow pointed apex. He was unable to describe the perigone lobes and the diaphragm.

Distribution — Borneo, only once found in NE Kalimantan, Sekerat Mts, in 1917.

Habitat — At 600–700 m altitude, according to Coomans de Ruiter, *Trop. Natuur* 22 (1933) 166.

Note — Because of the flattened rim of the disk this species is rather similar to *R. rochussenii*. It is, however, distinguishable by the possession of the processes on the disk and by the very rudimentary ramenta, like those of *R. patma*. The remaining material in alcohol is very fragmentary and a good complete description is not possible.

Rafflesia ciliata Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 64, pl. 9. — Type: *Witkamp* collection from Sekerat Mts, NE Kalimantan, no material found in BO.

All we can learn about this enigmatic species from the original description, based on a bud of 17 cm diam., is that the perigone lobes have numerous dense warts, the rammenta are simple or branched, not swollen at apex, the lower face of the diaphragm has only bristles, no warts, and the disk has many processes, pointed at the apex. The hairy laminae between the anther cavities and the shape of the anthers and many other details given by Koorders are shared by most species of *Rafflesia* and are of no diagnostic importance.

A collection from the same huge general region of the Sekerat Mts was made on the Sangkulirang Peninsula by Kostermans, Sept. 1957, near Mapula(?) vilage. It consists of a male bud of 14 cm diameter with 40 anthers. This would make it likely that this specimen either belongs to *R. keithii* or that *R. arnoldii* occurs all the way from SW and C to NE Kalimantan. In case future fieldwork on the Sekerat Mts would show that *R. keithii* is common there we have enough circumstantial evidence that specimens of that species were described by Koorders under the names *R. witkampii* and *R. ciliata*. The latter species name could be excluded from priority because of the lack of a convincing type specimen. It is not possible to solve this puzzle without the collection of new evidence in the field.

Rafflesia titan Jack, Appendix Descr. Mal. Plants I (1821), reprinted in Hook. Comp. Bot. Mag. 1 (1835) 259.

The reason William Jack made his own description of *Rafflesia* and gave the name *R. titan* to the plants collected for Raffles and by Raffles and him in the province of Bengkulu before he died on 15 September 1822 was revealed in a letter he wrote in May 1821 to Wallich in Calcutta. The letter was reprinted by Burkill in a paper in J. Straits Br. Roy. Asiat. Soc. 73 (1916) 148–268, and contains the following statement: “You must observe that though labelled an appendix to the Malayan Miscellanies it has been kept back till we hear what is done at home about the great flower (*Rafflesia*). If it is brought forward in England then this is to be suppressed and not published; if no, then this may be used in the event of the French getting hold of it, as a proof of priority of publication.”

From a letter he sent home 10 April 1820 [published by W. J. Hooker in Hook. Comp. Bot. Mag. 1 (1835) 135] we learn: “I lately sent to England a short account of some of my most interesting plants, to be noticed there in some way or other, including the sumatran gigantic flower, my two new Pitcher-Plants, the Camphor, the Sago and a new genus of mine, which Sir S. Raffles has forwarded for me, with the drawings of them, to Mr. Marsden, to make such use of them as he thinks best.”

It must have taken sail ships at least three months to reach England from Sumatra.

On 30 June 1820 Robert Brown read his famous paper on *Rafflesia* at a meeting of the Linnean Society of London and an excerpt of this was published November or December of that year in the Dutch magazine *Algemene Kunst en Letterbode* vol. 2, nr. 3, and probably also in the German journal *Flora*.

From the correspondence between Dr. D.J. Mabberley, Dr John Bastin and myself in 1984 and 1985 no convincing evidence has been produced that Jack's Appendix reached England before the Brown paper came from the press in May or June 1821 and was distributed at least to various scientific quarters. The most likely date of publication of Brown's paper should be June 1821 at the latest, not July, the earliest month of arrival of two reprints in India [see Merrill, *J. Arnold Arbor.* 33 (1952) 203]. A copy sent to Brown by Jack was mailed in a letter dated 23 May 1821 according to Mabberley in an unpublished note, a part of the correspondence, in which he wrote me (4 March 1985): "it would be a service to the literate world to have this name (*R. arnoldii* R. Brown) fixed for all time."

To take any further doubt away we can also argue that we now know that before 1940 there were at least two species of *Rafflesia* known from Bengkulu (see under *R. gadutensis* in this treatment) and that the description by Jack is not fully convincing us that he had not mixed data from two species in his species description and that only for *R. arnoldii* we have very clear drawings and a type specimen available to proof its true identity.

Rafflesia tuan-mudae Becc., Atti Soc. Ital. Sc. Nat. 11 (1868) 197; Nelle For. Borneo (1902) 166, illus.; Solms-Laubach, Ann. Jard. Bot. Buitenzorg 9 (1891) 239, t. 27, f. 4, 5, 9; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 66; Pawozan, Family Tree, For. Dept. Sarawak Internal Newsl. 18 (1988) 3–7, col. phot. — Type: *Beccari s.n.* (FI-B).

Medium-sized flowers c. 44–56 cm diameter. Lower face of diaphragm and ramenta much like *R. arnoldii* but perigone tubes with only about 5–8 whitish warts across the broadest part, these relatively smaller than those of *R. gadutensis*. Number of anthers not known.

Distribution — *Malesia*: W Sarawak (Mts Pueh, Gading, Rara).

Habitat — As described by Beccari (1902) in lowland Dipterocarp forest.

Notes — 1. Beccari and Solms-Laubach did not have a sharp concept of this entity. Beccari himself [*Nuovo Giorn. Bot. Ital.* 7 (1875) 70–75] reduced his species to *R. arnoldii* Brown but later on left it to Solms-Laubach (l.c. 1891) to revive it, mainly based on the smaller size of the flowers and fewer blots across the perigone lobes.

2. Coomans de Ruiter collected *Rafflesia* in SW Borneo, later in Bogor identified as *R. tuan-mudae*, but the flowers illustrated by him are good matches of *R. arnoldii*. However, the smaller form described by Beccari was later also found on Mt Rara by Dr. J. Mogeia (BO) and Dr. W.J.J.O. de Wilde (L). So it now appears to be a form restricted to three isolated mountains. As a widespread species *R. arnoldii* has greater variability in size and form than some species with smaller areas.

Rafflesia witkampii Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 61, pl. 7, 8. — Type: *Witkamp* collection, Sekerat Mts, NE Kalimantan (BO, in spirit).

This 'species' was described by Koorders merely on the basis of the study of a bud, 25 cm diameter, of a female flower. The column was expanded and a rupture in the tis-

sues between the annuli produced the 'wings' illustrated. Most likely the bud was left to dry out and later returned to a bottle with spirit. Several other 'distinctive' characters have no value because they were described from an immature bud. For the time being it is impossible to interpret this species as anything else than perhaps the female flower of *R. ciliata* Koord., collected at the same locality, an enigma itself. From the size of the bud we can exclude *R. pricei* as a possible identification. *Rafflesia keithii* would fit the size.

The species is possibly still present at the type locality though the site is doomed to disappear because of the planned establishment of a cement factory at that place. Other sites may still survive east of the Kutai National Park and in and around Sangkulirang. Ultimately the name may deserve priority over *R. keithii*.

RHIZANTHES

Rhizanthus Dumort., Anal. Fam. Pl. (1829) 14; Meijer & Veldkamp, Blumea 33 (1988) 329–342; Meijer in Kubitzki (ed.), Fam. & Gen. Vasc. Pl. 2 (1993) 561. — *Brugmansia* Blume in Van Hall, Bijdr. Natuurk. Wetensch. 2 (1827) 422, nom. illeg., non Pers. (1805). — *Zippelia* Rchb., Handb. Nat. Pfl.-Syst. (1837) 164, nom. illeg., non Blume ex Schult. & Schult. f. (1830). — *Mycetanthus* Rchb., Deut. Bot. Herb.-Buch (1841) 61, nom. illeg., superfl. — Type species: *Rhizanthus zippelii* (Blume) Spach.

Flowers unisexual or bisexual, buds pyriform, from a basal cupule attached to or arising from the roots or basal stem and aerial roots of the host, surrounded by three or four whorls of 5 scales, these sessile, imbricate, concave, more or less ovate, entire, brownish. *Perigone lobes* 16, valvate, with worm-like apices attached inside a cavity (crater) of the central column. *Anthers* in a ring around the lower margin of the column disk, about 38–50, each with 2 superimposed loculi. Male flowers with a rudimentary ovary, mature perigone tubes campanulate, radially striped in the center. *Fruits* hidden under dried-out flowers. *Seeds* with the same structure as those of *Rafflesia* [see Bouman & Meijer, Pl. Syst. Evol. 193 (1994) 187–212]. — **Fig. 10–12.**

Distribution — In *Malesia* 2 species (Sumatra, Peninsular Malaysia, Java, Borneo).

Ecology — The host of both species is in general *Tetrastigma papillosum* (Blume) Planch., sometimes also *T. leucostaphylum* (Dennst.) Alston ex Mabb. [= *T. lanceolarium* (Roxb.) Planch.].

Note — A very clever field investigation into the pollination of *Rhizanthus* (most likely *R. lowii*) in S Thailand and the Malay Peninsula (Perak) was reported by Bänziger (1996). He observed 900 visits of *Calliphoridae* (Bow flies) to 270 flowers and considers 6 species to be pollinators and the others non-pollinating visitors. His conclusion is that *Rhizanthus* just like *Rafflesia* mimics carrion in a pollination syndrome based on brood-site deception. Apparently eggs can be laid but the larvae starve to death. Insects are also lured to the nectaria at the base of the bayonets. As known to all observers, the flowers of *Rhizanthus* smell to the human nose much fainter than those of *Rafflesia*. See for other interesting details the original publication.

Reference: Bänziger, H., Nat. Hist. Bull. Siam Soc. 44 (1996) 113–142.

KEY TO THE SPECIES

- 1a. Flowers red-brown at anthesis, unisexual. Basal darker part of the bayonets covered with a velvety layer of c. 1.5 mm long, strongly branched antler hairs **1. *R. lowii***
- b. Flowers white at anthesis, bisexual, male with rudimentary ovary, or male. Basal part of the bayonets with short hairs only once or twice branched or only curved at apex **2. *R. zippelii***

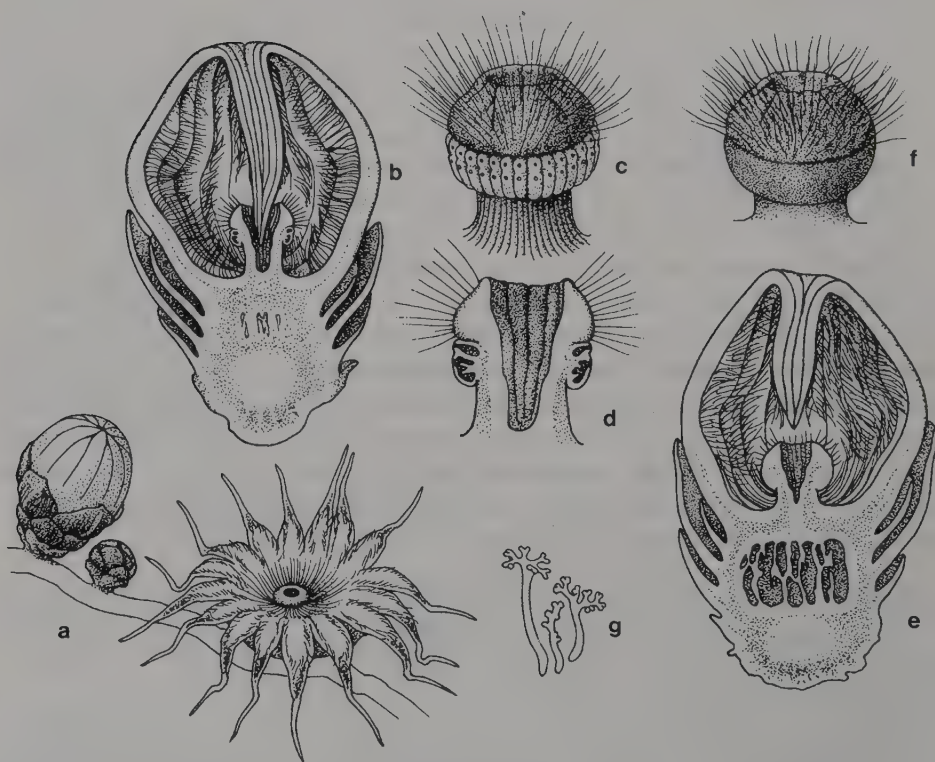


Fig. 10. *Rhizanthese lowii* (Becc.) Harms. a. Flowerbuds and open flower on stem or woody root of *Tetrastigma*. The mature bud left shows the cupula at base, the bracts, and the 16 valvate perigone lobes. The open flower shows the perigone and the narrow bayonets which in the bud were directed downwards and partly hidden in an apical cavity of the column; b. mature male flowerbud with rudimentary ovary; c. column of male flower, showing ring of anthers; d. section through the former; e. female flowerbud; f. column of female flower, stigmatic ring below the apex; g. ramenta from the glandular bases of bayonets from where they are often removed by frequent fly visits. Drawings by Janis Atlee, from photographs by W. Meijer, Kinabalu National Park, 1994.

1. *Rhizanthus lowii* (Becc.) Harms

Rhizanthus lowii (Becc.) Harms in Fedde, Rep. 36 (1934) 287; Corner & Watanabe, Illus. Guide Trop. Pl. (1969) 163. — *Brugmansia lowi* Becc., Atti Soc. Ital. Sc. Nat. 11 (1868) 198 ('lowi'); Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 101, t. 17, f. C – E; Merr., Enum. Born. Pl. (1921) 244; Ridl., Fl. Malay Penins. 3 (1924) 20, t. 137. — *Brugmansia zippelii* Blume var. *lowii* (Becc.) Hook. f. in DC., Prodr. 17 (1873) 113. — *Mycetanthus lowii* (Becc.) Hochr., Candollea 4 (March 1930) 188; Steenis, Bull. Jard. Bot. Buitenzorg III, 11 (June 1930) 18. — Type: *Low s.n. in Herb. Beccari* (FI holo; B). More extensive list of references in Meijer & Veldkamp, Blumea 33 (1988) 335.

Flowers always unisexual, concolorous white to reddish (on Mt Leuser also with a white tube and brown lobes). Buds ovoid-pyriform, up to 12 by 7 cm; open flowers infundibuliform, 18–35 cm in diam. *Perigone lobes* 6–12 mm wide at base, gradually narrowed, basal hairy part c. 3 cm long, gradually narrowed into the geniculate, c. 2.5 cm by 1–2 mm apical appendage, the upper part of c. 6.5 cm without long hairs. *Perigone tube* inside long hairy below, the upper c. 2 cm with short hairs with an antler-like shape, male flowers with 50–60 lines, corresponding to the number of anthers. Central column c. 2 cm long, in female buds with a c. 0.5 by 1 cm diameter stipe, and a globular more or less depressed apex, 1–1.5 by 1.5–2 cm diameter, apical cavity c. 1 cm wide and deep. *Male flowers* with a c. 7 cm broad ring of 50–60 anthers around the base of the globular disk; stipe with c. 50–60 ridges; ovary rudimentary. Columnar disk of *female flowers* with a c. 7 mm wide stigmatic hairy zone along base; stipe not ridged; ovary c. 1.5 by 3 cm diam. *Fruit* not seen. — **Fig. 10, 11.**



Fig. 11. *Rhizanthus lowii* (Becc.) Harms. N Sumatra, Ketambe (de Wilde 12148). Photograph W.J.J.O. de Wilde, 1972.

Distribution — Sumatra (Aceh, Gajolands, Sibolangit, Bengkulu, Palembang, Lampung), Peninsular Malaysia (Pahang, Perak, Trengganu), Borneo (Sarawak, Sabah, W and E Kalimantan).

Habitat — Lowland Dipterocarp and hill forest, 200–1500 m altitude.

Ecology — Parasitic on *Tetrastigma papillosum* (Blume) Planch.

Notes — 1. Although in the footsteps of Beccari the epithet is often written as *lowii*; ICBN Art. 73.10 and Rec. 73 C 1 make it clear that *lowii* is the correct form.

2. Bänziger, Nat. Hist. Bull. Siam Soc. 43 (1995) 337–365 argues that there is only one species (*R. zippelii*) in this genus. However, he most likely never saw the real *R. zippelii*. He based his concept of it on the wrong identification by Meijer & Veldkamp (1988) of a specimen collected by Molesworth in a locality in Malaya which Bänziger also visited himself.

2. *Rhizanthus zippelii* (Blume) Spach

Rhizanthus zippelii (Blume) Spach, Hist. Nat. Vég. 10 (1841) 554; Backer & Bakh. f., Fl. Java 1 (1963) 166. — *Brugmansia zippelii* Blume in Van Hall, Bijdr. Natuurk. Wet. 2 (1827) 422; Miq., Fl. Ind. Bat. 1, 2 (1859) 684; Koord., Bot. Overz. Raffles. Ned.-Indië (1918) 94, t. 15, f. A–D. — *Zippelia brugmansia* Rehb., Handb. Nat. Pfl.-Syst. (1837) 164, nom. illeg., superfl. — *Mycetanthus zippelii* (Blume) Hochr., Candollea 4 (March 1930) 188; Steenis, Bull. Jard. Bot. Buitenzorg III, 11 (June 1930) 18. — Type: *Zippel* s.n. (L holo, spirit).

Brugmansia bakhuisenii Heinr., Denkschr. Akad. Wiss. Wien, Math.-Naturw. Kl. 78 (1906) 63, 66, t. 1, f. 1–4, t. 3, f. 3–5, 7, nom. prov., illeg.; Backer & Bakh. f., Fl. Java 1 (1963) 166, in obs. — Voucher: *Bakhuisen van den Brink* s.n. (IB).

More extensive list of references in Meijer & Veldkamp, Blumea 33 (1988) 339.

Flowers unisexual or bisexual, buds up to 10 by 5 cm, pinkish, smooth, at anthesis first concolorous white, later bright red or brown, 8–21 cm in diameter incl. the worm-like apical appendages. *Perigone lobes* c. 2.5 by 1.5 cm at base, free part 4.5–5 cm long (excl. the appendages), apex c. 0.5 cm thick; in upper c. 1.8 cm with short brown hairs with antler-shaped apices; lobes curved downwards touching the substrate, initially united at base in groups of 3 or 4, later free, splitting on the outside to c. 1.5 cm from the base of the tube, on the inside to c. 3 cm, forming a thin c. 1.5 cm long membrane. *Perigone tube* 2–2.5 cm long, inside with 46–55 brown lines around the column, fading out towards the base of the lobes; base and inside of the tube with 5–7 mm long hairs, apically slightly hooked; column c. 2 cm long, base narrow, c. 1 cm thick, head globular, 1.8–2 cm wide, apex purplish brown, hairy, crater 0.5–0.9 cm diam. *Anthers* 38–50. *Ovary* with stigmatic ring c. 0.5 cm high, white. *Fruit* subglobose, up to 6.5 cm diameter, brown, hidden by the dark-brown dried perianth. *Seeds* oblong, c. 0.75 by 0.3 mm, appendage oblong, about half as long as the seed. — **Fig. 12.**

Distribution — Sumatra (Aceh, W Sumatra, Bengkulu, Lampung), Peninsular Malaysia (Perak), Borneo (W Kalimantan, from Sabah and Sarawak no firm records), W Java (Ciapus canyon, Mt Salak).

Habitat — Primary or secondary forests, often along streams on deep alluvial soils, 500–1500 m altitude.



Fig. 12. *Rhizanthus zippelii* (Blume) Spach. a. Open flower, wine-red in colour; b. male flower in length section, ovary rudimentary, no trace of stigma ring around the column; c. bisexual flower in length section, ovary below the column which shows anthers as well as a stigmatic ring above them; d, e. detail of the column, with stigmatic ring; f. ripe fruit, partial cross section, thousands of seeds attached to the convoluted parietal placenta; g. rameta at the base of the bayonets. Drawing by Janis Atlee: d, e after Blume, g after Heinricher; others from photographs made by W. Meijer in Sumatra, Ulu Gadut forest.

Ecology — Host is usually *Tetrastigma papillosum* (Blume) Planch., occasionally *T. leucostaphylum* (Dennst.) Alston ex Mabb. (names based on herbarium study by the present author). Van der Pijl [Trop. Natuur 22 (1933) 55] reported a species of *Villebrunea* sp. (*Urticaceae*) as host.

Notes — 1. Blume's original illustration of the flower reproduced repeatedly in the literature has given rise to some confusion because the flower shown had not yet fully expanded, the perianth lobes still sticking together in groups of 3 to 5.

The first illustrations of *Rhizanthus lowii* showed flowers with all perianth lobes free from each other. Heinricher [Denkschr. Akad. Wien, Math.-Naturw. Kl. 78 (1906) 63, 66, illus.], who found *R. zippelii* in its natural situation, was considering to describe it

as a new species (*R. bakhuiizenii* ?). Probably Blume's flower was produced in the laboratory after the host and buds were dug up from the jungle. There is nothing to indicate that the flower from Mt Salak represented a different species than those later discovered at all other localities.

2. Backer & Bakhuizen f. (1963) distinguished two forms: *R. zippelii* s.s. with white or flesh-coloured perianth, etc. from the Salak, and '*Brugmansia bakhuiizenii*' with bright red perianth, etc. from Mt Gede, Cidadap, and Garut. The latter, however, is nothing else than the phase shown by flowers on the second or third day of flowering.

3. Since 1940 there have been no more reports of this species from Java (pers. obs., Kostermans pers. comm.). In October 1981 Meijer saw still some specimens of *Tetragium papillosum* in the steep Ciapus Canyon on Mt Salak. Cultivation and tree plantations had replaced the original forest at the margin of the canyon. No botanists have penetrated into the canyon in the past 60 years, but Meijer found in August 1996 that guides are leading parties into it.

BORAGINACEAE

(H. Riedl, Vienna)¹

Boraginaceae Juss., Gen. Pl. (1789) 128 ('*Borragineae*'); Brand in Engl., Pflanzenr., fam. IV.252 (1921) 1–183 (*Cynoglosseae*); *ibid.* (1931) 1–236 (*Cryptantheae*); Heine in Fl. Nouv.-Caléd. 7 (1976) 95–118; I.M. Johnston, Contr. Gray Herb. 73 (1924) 42–73; Ridl., Fl. Malay Penins. 2 (1923) 438–442; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 687–698; Van Royén, Pac. Sc. 29 (1975) 79–98.

Trees, shrubs, subshrubs, woody climbers, perennial or annual herbs usually covered by hairs or bristles on the herbaceous parts, woody species sometimes entirely glabrous. *Leaves* alternate, very rarely opposite (in *Tournefortia*), exstipulate, undivided, usually entire, in a very few species serrate, with reticulate venation of which only the main nerves are clearly detectable in most cases. *Inflorescence* either a simple cyme or compound, cymes arranged dichotomously or in racemes or panicles, with or without bracts, terminal or lateral, sometimes single flowers in the axils of upper leaves. *Flowers* hermaphroditic, rarely unisexual and plants monoecious, composed of calyx and corolla, pentamerous, rarely tetramerous, actinomorphic, in some genera slightly zygomorphic. *Calyx* campanulate to cup-shaped, lobes entirely free or more or less coherent, sometimes accrescent or spreading after flowering, sessile or distinctly stalked. *Corolla* coherent in lower part (tube), lobes free, erect or spreading in the upper part (limb), with an intermediate, gradually widening zone (throat), tubular, campanulate to funnel-shaped or rotate, lobes usually imbricate in bud, rarely valvate, bent into the throat (in some *Heliotropium* spp.) or contorted (in *Myosotis*). In many genera, scale-like invaginations (fornices) present in the throat. In some genera, a basal nectary ring, scale-like appendages (that are not hollow invaginations) or variously distributed hairs inside the corolla present. *Stamens* of the same number as corolla lobes, alternating with them, included in or exerted from the corolla; anthers sessile or on distinct filaments, sometimes with a sterile tip of connective tissue or produced to an awn-like structure, awns of one flower twisted or not, anthers bilocular, dorsally fixed to the corolla or the filament, opening longitudinally. *Ovary* superior, often fixed either to a disc-like base or base produced to a conical or pyramidal structure (gynobasis), bicarpellate as a rule, undivided, entire or with four deep furrows, breaking into two biovulate halves or into four uni-ovulate mericarps ('nutlets'), sometimes part of the locules aborted, rarely a greater number of carpels developed (e.g., in *Trigonotis procumbens*); placentation axillary; ovules erect or nearly horizontal, rarely pendent. *Style* single, either terminal on the undivided ovary or free at last on top of the 4-partite ovary, or fixed basally on the disc-like base between the nutlets or apically on the conical to pyramidal gynobasis, undi-

1) With contributions by: P. Baas, Leiden (vegetative anatomy), R.W.J.M. van der Ham, Leiden (palynology), R. Hegnauer, Leiden (phytochemistry and chemotaxonomy). Most drawings are by Ms. N. Spitteler; origin of photographs is as indicated.

vided or once to twice forked, sometimes cleft nearly to the base; stigma absent or disc-to cushion-shaped terminating the style, or (in *Heliotropium* and *Tournefortia*) forming a ring round the style at various levels (for convenience' sake the ring together with the terminal part of the style above the ring is called stigma as a rule); heterostyly rather frequent (in groups outside Malesia). *Fruit* drupaceous or a berry or divided into 2–4 mericarps surrounded by a hard outer wall, sometimes adherent to the style and separating with an awn; surface smooth, warty, or rugulose, often tuberculate or spiny, sometimes divided into a disc-like outer and a convex inner side, the outer disc surrounded by a thickened margin or not, sometimes glochids present on the whole or certain parts of the surface or nutlets winged. *Seeds* usually without albumen.

DISTRIBUTION

About 100 to 115 genera with a total of about 2,400 species in all climatic regions of the earth. The woody genera of subfamilies *Cordioideae*, *Ehretioideae* and *Heliotropioideae* are predominant in tropical and subtropical regions, *Heliotropium* is widespread in tropical and temperate regions, while herbs and subshrubs belonging to *Boraginoideae* are most numerous in temperate regions, in the tropics mainly confined to higher altitudes or growing as weeds and also represented in the arctic with a few species (involves only *Boraginoideae*).

In the Malesian region, 12 genera are indigenous, two more introduced. Of these, *Crucicaryum* is of rather doubtful value and only known from one collection, which has been lost. *Pteleocarpa*, sometimes regarded as a member of *Boraginaceae*, is not included in this family by the present author. The number of species acknowledged in this account, is 77, of which 64 or 65 are indigenous, the other 12 or 13 having been introduced either for economical and/or ornamental uses or as weeds.

HABITAT

Boraginaceae are widespread in a great number of different habitats from sandy sea shores to mountain forests, wet meadows, desertic or semidesertic regions and stony slopes. In tropical countries, they are absent from lowland rain forests as a rule as well as from vegetation types derived from them. Subfamily *Boraginoideae* is confined to mountainous areas at higher altitudes in the tropics and subtropics as mentioned above. Several species are introduced into new areas of distribution as weeds.

ECOLOGY

Pollination is performed by insects of various groups in a great majority of cases though special adaptations to particular pollinators are lacking. Faucal appendages prevent insects with a short proboscis from pollinating the flowers in many genera, however. These appendages serve as guide to the nectar in the basal part of the corolla. Selfing is observed in a number of taxa, but is prevented by heterostyly in others. Heterostyly is combined with self-incompatibility as a rule, in some genera also with pollen dimorphism. In large-flowered *Cordia* species bats may act as pollinators.

There are several ways of dispersal found within the family. Nutlets bearing glochids are well adapted to epizoochorous dispersal. Comparatively small, hard nutlets are eaten by birds and transported in their digestive tract over longer or shorter distances, while the fruits of *Cordia* are partly digested by mammals and the endocarp is excreted in a viable state. Species of the sea coast such as *Tournefortia argentea* with a spongy pericarp are dispersed by seawater. Winged nutlets are transported by the wind. The same is true sometimes in plants with single surviving nutlets that are shed together with the enlarged calyx.

FOSSILS

There are only a few records of pollen of *Cordia* and *Tournefortia* from the Oligocene and Miocene from Mexico, Puerto Rico and the Marshall Islands. Nutlets of still extant and of extinct genera have been reported from the Miocene. Among the latter, especially *Prolithospermum* is of interest for the phylogeny of present-day *Boraginaceae* as demonstrated by Johnston (1954).

Literature: Gabel, M.L., Amer. J. Bot. 74 (1987) 1690–1693. — Graham, A. & D.M. Jarzen, Ann. Missouri Bot. Gard. 56 (1969) 308–357; *ibid.* 63 (1976) 787–842. — Johnston, I.M., J. Arnold Arbor. 35 (1954) 1–81.

MORPHOLOGY AND ANATOMY

Hairs — Hairs are among the most generally distributed features in the family. Unicellular hairs are always present, but they are not the only type of hairs in many species. Typical for unicellular hairs are agglomerations of calciumcarbonate or cystoliths in their lumen. To maintain their flexibility, there are various devices, most often a specific distribution of thin and thickened segments of the cell wall. In many cases, most characteristically in members of tribe *Lithospermeae*, the hairs are surrounded by one to several circles of so called ‘accessory cells’ with calcified cell walls, that may also be different in the ratio of length to width from other epidermal cells. Widespread are bristle-like hairs with one longitudinal series of cells the terminal cell of which may be horizontal or oblique. These are glochids mainly found on fruits in order to attach them to the fur of animals. Other types of hairs less common are capitate hairs which are characterized by undivided heads in *Boraginaceae*, stellate hairs and hairs composed of more than one series of cells.

Literature: Hummel, K. & K. Staesche, Verbreitung Haartypen. In: Handb. Pflanzenanat., ed. 2, IV, 5 (1962).

Inflorescence — The most peculiar morphological feature of *Boraginaceae* is their inflorescence, which has sometimes been called ‘boragoid’. It is sympodial with a straightened axis. The main axis is terminated by a single flower. From the axil of the uppermost leaves one or two side branches originate, which in turn are terminated by a flower. In *Boraginaceae*, either single bracts are developed or bracts are utterly suppressed. The composite axis of the inflorescence is continued by a branch originating from the axil of

the bract if present. This is not obvious in most cases, however, as the true origin of the side branch is obscured by concaulescence, that means, the two axes are connate in part. In most members of *Heliotropioideae* and *Boraginoideae* at least, the flowers are all directed to one side, so that the resultant inflorescence is scorpioid at least when young, the terminal flowers being arranged in a whorl. Morphologically, this type of inflorescence can be derived from that of many *Solanaceae*, in which normally two leaves or bracts are developed at the point of origin of the side branch.

Literature: Troll, W., Prakt. Einf. Pflanzenmorph. 2 (1957) 357–361.

Fruit attachment — While the undivided or divided fruits are attached to the receptacle and separate from it at maturity as a rule in *Cordioideae*, *Ehretioideae* and *Heliotropioideae*, in *Boraginoideae* part of the outer layers of the wall of the carpel remains coherent with the receptacle, so that at maturity the wall is split. Sometimes, these outer tissues form a conical to subulate structure in the centre between the separating nutlets, that bears the style and is called gynobasis by most authors. It has wrongly been interpreted as part of the receptacle.

Literature: Hilger, H., Bot. Jahrb. Syst. 105 (1985) 323–378.

Anatomy of the nutlets — The ovary of *Boraginaceae* is supplied by 10 vascular bundles, which may be modified in relation to special morphological features of the nutlets, such as wing formation. The wall of the nutlets displays a constant sequence of a number of distinct layers. The outermost single-celled layer or exocarp produces the various types of sculpturing on the surface and may be multilayered in the protuberances thus formed. In *Lithospermeae* it consists of palisade-shaped sclereids. The wall thickenings are typically undulated. In most groups the following mesocarp is composed of parenchymatous cells, while in *Lithospermeae* there is an outer part of elliptic sclereids in several layers and an inner parenchymatous part. In *Trichodesma*, the innermost layer is thick-walled. In some groups, especially *Cynoglosseae*, the endocarp has U-shaped thickenings, while it is thin-walled in most other groups. It is always single-layered. The seed coat itself consists of thin-walled cells covered by a cuticle or not.

Literature: Lawrence, J.R., Amer. J. Bot. 24 (1937) 433–444. — Roth, I., Encycl. Plant Anat. 10/1 (1977) 330–336 (earlier literature is reviewed in detail in this publication).

VEGETATIVE ANATOMY

(P. Baas)

Leaf anatomy — The leaf anatomy of the Malesiana *Boraginaceae* is very poorly known. The account given below derives from the general family survey by Metcalfe & Chalk (1950), with additional data from Inamdar & Patel (1973), Patel & Inamdar (1971), and Uphof et al. (1962).

Indumentum diverse, but typically including unicellular hairs containing cystoliths ('boraginaceous hairs', causing the typical roughness of the leaf surface); non-lithocyst

unicellular and uniseriate hairs also occur as well as branched multicellular hairs (*Cordia* p.p.) and short- or long-stalked glandular hairs with unicellular heads (e.g. in *Coldenia*, *Cordia* p.p., and *Heliotropium*). Stomata usually anomocytic, but anisocytic, paracytic and diacytic types also occur, often in the same leaf, as well as stomata with a single subsidiary cell. Mesophyll isobilateral or dorsiventral, occasionally including sclereids in *Cordia* spp. Vascular bundles of the veins embedded in the mesophyll or vertically transcurrent through sclerenchymatous bundle sheath extensions in *Cordia* p.p., *Ehretia*, *Heliotropium* p.p., and *Tournefortia*. Vascular system of midrib and petiole ranging from a single strand to a cylinder of vascular bundles enclosing medullary bundles. Crystals usually present as either crystal sand, solitary crystals or clusters and druses.

Wood anatomy — For a full bibliography on the wood anatomy of *Boraginaceae*, see Gregory (1994). Selected references for Asian *Boraginaceae* are Baas et al. (1984), Burgess (1966), Gottwald (1982, 1983), Heubl et al. (1990), Ilic (1991), Kanehira (1921), Metcalfe & Chalk (1950), Miller (1977), Moll & Janssonius (1926), Pearson & Brown (1932), Sudo (1963, 1988) and Versteegh (1968). Only the wood anatomy of *Cordia*, *Ehretia*, *Pteleocarpa*, and *Tournefortia* is well documented; that of the other Malesian genera (mainly herbaceous ones) is very poorly known.

Growth rings range from absent to distinct (and are then marked by thick-walled late-wood fibres, marginal parenchyma, and/or ring-porosity). Vessels mostly diffuse; exclusively solitary in *Pteleocarpa*; solitary and in radial multiples in other genera, latewood vessels in *Ehretia* also in clusters and in an ulmiform to dendritic pattern. Perforations all simple, or with sporadic reticulate plates in *Cordia* spp. Intervessel pits vestured (*Pteleocarpa*) or non-vestured (other Malesian genera as far as known), alternate; vessel-ray and vessel-parenchyma pits similar but half-bordered or (partly) enlarged or even perforated in *Cordia* p.p. Helical thickenings present in some narrow vessels of *Ehretia*. Vasicentric tracheids present in *Ehretia*. Fibres either with distinctly bordered pits (*Pteleocarpa*) or with minutely bordered pits (other genera), mostly non-septate, but some septate fibres present in *Cordia* p.p. and *Ehretia* p.p. Parenchyma abundantly paratracheal to banded in *Cordia*, predominantly apotracheal and diffuse-in-aggregates in *Ehretia*, narrowly banded and paratracheal in *Tournefortia*, and in fine unilateral paratracheal lines in *Pteleocarpa*. Rays (1–)2–3-seriate in *Pteleocarpa* and *Tournefortia*, up to 4–6-seriate in *Cordia* and *Ehretia*, heterocellular with few rows of square to upright marginal cells to homocellular in some species of *Cordia* and *Tournefortia*. Crystal sand and/or prismatic crystals in ray cells, axial parenchyma and/or tyloses of *Cordia* p.p. Heubl et al. (1990) also recorded clustered crystals in the wood of some taxa but probably only observed them in pith or bark and not in the secondary xylem. Parenchyma and fibres (weakly) storied in *Cordia* p.p. and *Tournefortia*.

Taxonomic note — As emphasised by Gottwald (1982) the genus *Pteleocarpa* is wood anatomically aberrant in the *Boraginaceae* on account of its solitary vessels, fibre pitting (fibre-tracheids) and parenchyma distribution, supporting the exclusion of this genus from the *Boraginaceae* (cf. Veldkamp 1988). As demonstrated by Gottwald (1983),

Heubl et al. (1990) and Patel & Inamdar (1971) the anatomical diversity within the *Boraginaceae* is of great, yet largely untapped, systematic potential.

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PALYNOLOGY

(R.W.J.M. van der Ham)

Erdtman et al. (1961) considered the *Boraginaceae* as rather stenopalynous. However, in the last decades it appeared to be one of the more eurypalynous families, even in a more strict taxonomic (*Boraginoideae*) or geographic (Malesia, NW Europe) delimitation. A single work dealing with the entire family is not available. Due to its heterogeneity, it is hardly possible to characterise the family in a comprehensive description. Based on a literature survey covering 80 genera (c. 3/5 of the total number) listed in the bibliographic index to angiosperm pollen (Tissot & Van der Ham 1994) characteristics and remarkable pollen types of all subfamilies and tribes are given. All genera surveyed and a selection from the literature are mentioned. The term heterocolpate indicates the occurrence of compound apertures (colpi with endoapertures) alternating with simple apertures (relatively long colpi).

Pollen of the *Cordioidieae* is oblate-spheroidal to subprolate (*Auxemma*, *Patagonula*: 18–25 µm; *Cordia*: 28–52 µm) and usually 3- (or 4-) colp(oid)ate (Heubl et al. 1990; Nowicke & Miller 1990). Section *Varronia* of *Cordia* has 3-porate pollen. Ornamentation is striate-reticulate, reticulate with scabrae, irregularly striate, rugulate or variously echinate or clavate. Seven pollen types based on aperture and ornamentation features can be distinguished.

Pollen of the *Ehretioideae* (*Bourreria*, *Carmona*: own observations, *Coldenia*, *Ehretia*, *Halgania*, *Lepidocordia*, *Rotula*, *Saccellium*, *Tiquilia*) is prolate-spheroidal to subprolate (15–50 µm) and usually (2- or 3-) colp(oid)ate, mostly with relatively thin mesocolpium centres: pseudocolpi (Heubl et al. 1990; Nowicke & Miller 1990; Sahay

1979). The colpi in *Rotula* pollen each have two poroid endoapertures, and are sometimes fused at the poles. *Coldenia*, which shows more affinities to the *Boraginoideae* than any other genus of the *Ehretioideae*, has 6-heterocolpate pollen (Qureshi & Khan 1985). Most *Ehretioideae* can be distinguished from most *Cordioideae* by the presence of pseudocolpi. *Lepidocordia* pollen is 3-colporate without pseudocolpi and perforate (Miller & Nowicke 1990), and is therefore in the *Ehretioideae* nearest to that of the problematical genus *Pteleocarpa* (not accepted as a *Boraginaceae* in the present work). *Pteleocarpa* pollen is deviating in possessing small endoapertures with acuminate lateral sides, a more reticulate tectum and a more developed infratectum (Lobreau 1969, 1975). *Saccellium*, tentatively assigned to the *Cordioideae* by Takhtajan (1987), has pollen much alike that of *Patagonula*.

Pollen of the *Heliotropioideae* is oblate-spheroidal to prolate (13–45 µm). *Ixorhea* (Di Fulvio 1980) and *Heliotropium* pollen are 6-heterocolpate, except for *H. indicum* which is 3-brevicolporate (Sahay 1973). Ornamentation is psilate/perforate in these genera. Pollen of *Tournefortia* is strikingly divergent. Four types have been distinguished (Nowicke & Skvarla 1974). The aperture system is mostly 6-heterocolpate or 3- (or 4-) colporate and the ornamentation more or less psilate. One type is 3-porate with clavate ornamentation. Another type has conspicuous psilate polar caps and protruding apertures. Pollen morphology does not support the separation of the *Argusia/Mallotonia/Messerschmidia* group. It confirms the close relationship with *Heliotropium*. Most *Heliotropioideae* can be distinguished from the *Cordioideae* and *Ehretioideae* by their 6-heterocolpate pollen. Within the family the 3-porate condition is restricted to a few species of *Cordia* and *Tournefortia*.

Pollen of the monotypic *Wellstedioideae* is suboblate (15–20 µm), 3 colporoidate, with a hexagonal equatorial outline (Erdtman 1952), which suggests the presence of pseudocolpi. According to Hunt (1969) the pollen of *Wellstedia* is not boraginaceous (s.s.) but more ehretiaceous, being fairly similar to that of for example *Ehretia rigida*.

The *Boraginoideae*, being the largest subfamily, is clearly the most diverse. Usually its pollen is distinctly prolate (5–65 µm), often more or less rectangular to equatorially constricted (Clarke 1977; Díez 1987). Of all dicots several species of *Myosotis* and *Trigonotis* have the smallest pollen grains ($P \times E = 5 \times 2$ µm). The ornamentation is mostly psilate to scabrate, and often slightly different in the equatorial zone (ectocingulus). A basic distinction is between tribes with colporate pollen (*Lithospermeae*, *Boragineae*, *Trichodesmeae* p.p.) and tribes with heterocolpate pollen (*Eritrichieae*, *Cynoglosseae*, *Trigonotideae*, *Myosotideae*).

The *Lithospermeae* (*Alkanna*, *Arnebia*, *Buglossoides*, *Cerithe*, *Cystostemon*, *Echiochilon*, *Echium*, *Lasiarrhenum*, *Lithodora*, *Lithospermum*, *Lobostemon*, *Macromeria*, *Maharanga*, *Moltkia*, *Onosma*, *Onosmodium*) have (2–)3–7(–11)-colporate variously shaped pollen. *Alkanna*, *Cystostemon*, *Echium*, *Lobostemon*, *Onosma* spp. and *Onosmodium* have heteropolar pear-shaped pollen (see also Díez et al. 1986; Pérez de Paz 1995; Popova & Zemskova 1995). *Echiochilon* pollen is 2-colporate. *Lithospermum* pollen is heteropolar in having the endoapertures situated near one of the poles. In *Arnebia* pollen the colpi are very wide, diporate and sometimes fused at the poles (Qureshi

et al. 1989). Syncolpate pollen is also found in *Onosma* spp. (Ning et al. 1995). Pollen dimorphism occurs in many heterostyled *Arnebia* species (Nowicke & Miller 1988).

The *Boragineae* (*Anchusa*, *Borago*, *Elizaldia*, *Gastrocotyle*, *Nonea*, *Pentaglottis*, *Pulmonaria*, *Symphytum*, *Trachystemon*) the pollen is (3-)4-6(-15)-colporate and never constricted (see also Harmata 1977, 1981; Ning et al. 1992). In most genera the endoapertures may be fused to form a continuous circular aperture (endocingulus). *Borago* pollen has complex apertures and very distinct columellae (Ben Saad-Limam & Nabli 1984).

The *Eritrichieae* (*Amsinckia*, *Asperugo*, *Craniospermum*, *Cryptantha*, *Eritrichium*, *Hackelia*, *Lappula*, *Microula*, *Myosotidium*, *Nesocaryum*, *Plagiobotrys*, *Rochelia*, *Selkirkia*) usually have 6(-8)-heterocolpate constricted pollen (see also Díez et Valdés 1991; Marticorena 1968; Ning et al. 1993). In *Amsinckia* it is elliptic or pear-shaped. *Craniospermum* might be 3-colporate (Johnston 1956). In *Lappula* and *Rochelia* the three endoapertures are offset from the equatorial plane, two to one pole and one to the other; in *L. patula* each colpus has two pores.

Pollen of the *Cynoglosseae* (*Actinocarya*, *Antiotrema*, *Cynoglossum*, *Gyrocarium*, *Lindelofia*, *Omphalodes*, *Paracaryum*, *Pardoglossum*, *Pectocarya*, *Rindera*, *Solenanthus*, *Thyrocarpus*) is much alike that of the *Eritrichieae*: 6-heterocolpate, although mostly not constricted (Barbier & Mathez 1973; Díez & Valdés 1991; Marticorena 1968). *Cynoglossum* spp., *Pardoglossum* and *Rindera* have poro-colpate pollen: three compound pori alternating with three simple colpi (Clarke et al. 1979).

Pollen in the *Trigonotideae* (*Bothriospermum*, *Brachybotrys*, *Mertensia*, *Moltkiopsis*, *Neatostema*, *Ogastemma*, *Omphalotrigonotis*, *Sericostoma*, *Sinojohnstonia*, *Trigonotis*) is diverse. Usually it is 6(-8)-heterocolpate, but it is 6-colporate in *Moltkiopsis* (Popova & Zemskova 1995), (6-) 7- (8-)colporate in *Neatostoma* (Díez et al. 1986), 2-colporate in *Sericostoma* and 3-(col?)porate in *Ogastemma*. Palynologically these genera would be better placed in the *Lithospermeae*, where they were initially accommodated by Johnston (1953, 1957). The 3-colporate pollen with distinctly protruding apertures of *Omphalotrigonotis* (Xi 1984) does not fit in the *Trigonotideae*, nor in any other tribe of the *Boraginoideae*. It rather resembles the pollen of *Tournefortia setacea* (Nowicke & Skvarla 1974, fig. 14) of the *Heliotropioideae*.

Pollen in the *Myosotideae* (*Myosotis*) is diverse: 6-, 8-, 10- (12-)heterocolpate, sometimes (para)syncolpate, constricted or not (Díez & Valdés 1991; Grau & Leins 1968; Grau & Schwab 1982).

Pollen in the *Trichodesmeae* is 6-heterocolpate (*Suchtelenia*) or 3-colpor(oid)ate (*Cacania*, *Trichodesma*) and not constricted (Barbier & Mathez 1973; Bonnefille & Riollot 1980).

Although palynologically most of the subfamilies can be characterised fairly well, their mutual relationships are less clear. The 3-colpor(oid)ate pollen in the *Cordioideae* is a basic angiosperm pollen type, and might be considered basic in the *Boraginaceae* as well. The frequent occurrence of pseudocolpi makes the *Ehretioideae* more derived. However, it is unknown whether the common 6-heterocolpate type of the *Heliotropioideae* and *Boraginoideae* evolved from a 3-colpor(oid)ate/pseudocolpate type like in the

Ehretioideae (and *Wellstedioideae*?) or was derived 'de novo' from a basic 3-colporate type as in the *Cordioideae*. *Coldenia*, intermediate between the *Ehretioideae* and the *Boraginoideae*, has 6-heterocolpate pollen, which suggests derivation from the pseudocolpate type. In contrast, *Lepidocordia*, intermediate between *Ehretioideae* and *Heliotropioideae*, has 3-colporate pollen without pseudocolpi, which indicates a 3-colporate origin of the heterocolpate type. It would be interesting to analyse *Heliotropium* and *Tournefortia*, where both colporate and heterocolpate pollen occur within a single genus. Significant for a more inclusive point of view is whether the *Lithospermeae* (colporate) or the *Trigonotidae* (heterocolpate) are considered basal in the *Boraginoideae* (see discussion by Al-Shehbaz 1991). It appears that pollen morphology has a clear potential in a phylogenetic analysis, as it characterises groups of taxa on various taxonomic levels.

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EMBRYOLOGY

Embryology has played a major part in the discussion whether *Boraginaceae* should be divided into at least two separate families or not. In subfamily *Boraginaceae* the endosperm may be nuclear, cellular or of an intermediate type, in the remaining subfamilies (as far as is known) it is always cellular. In *Boraginoideae*, an endosperm haustorium is lacking, while it is present in the remaining subfamilies. The suspensor is short in *Boraginoideae*, long in the rest. As already mentioned, pollen characters are not necessarily correlated with embryology, as *Trichodesma* likewise has two nuclei instead of three as in most of the other *Boraginoideae*. Mainly for embryological reasons, *Heliotropiaceae*

Schrader as a separate family are advocated by several authors. Position of the embryo is correlated to attachment of nutlets and not always easy to interpret, therefore.

Literature: Di Fulvio, T.E., Kurtziana 12–13 (1979) 101–112. — Svensson, H.G., Uppsala Univ. Årsskr. Matematik och Naturvet. 2 (1925) 1–175, f. 1–15.

CHROMOSOMES

Polyploidy is confined to a certain limited number of genera within the family, while aneuploidy seems to be of great importance. In *Cordioideae*, only diploids are known with $n = 8, 14, 16$. In *Ehretioideae*, the basic number x may be 7–11, 13 and 21. In *Heliotropioideae* and *Boraginoideae* together, all basic numbers are known from $x = 4$ to 13. While it is often argued that the base number of the family as a whole is 12 because of its wide distribution within *Boraginoideae*, this is certainly not the case for the other subfamilies, in which $x = 8$ is much more likely the primary base number. There is no clear correlation between aneuploidy and systematic position within subfamily *Boraginoideae*, though $x = 12$ is most common in *Cynoglosseae* and probably also in *Eritrichieae*, while it is much less common in *Lithospermeae*. The lowest diploid number known in the family is $2n = 8$, while the highest is $2n = 144$.

Literature: Al-Shehbaz, I.A., J. Arnold Arbor., Suppl. Ser. 1 (1991) 1–169. — Britton, D.M., Brittonia 7 (1951) 233–266. — Lewis, W.H., Polyploidy: biological relevance (1980) 241–268. — Takh-tajan, A., Systema Magnoliophytum (1987) 244–247.

PHYTOCHEMISTRY AND CHEMOTAXONOMY

(R. Hegnauer)

Pyrrolizidine alkaloids and quinonoid or phenolic compounds biogenetically derived from C-prenylated or -geranylated or -farnesylated 4-hydroxybenzoic acid are the most striking secondary metabolites of this family. The isomeric red pigments alkannin and shikonin are the best known representatives of such hydroxybenzoic acid derivatives. Synthesis and accumulation of pyrrolizidines and of alkannin-related compounds occur in all four subfamilies commonly accepted within the *Boraginaceae*; they form a biochemical link between *Cordioideae*, *Ehretioideae*, *Heliotropioideae* and *Boraginoideae*.

Boraginoideae and *Heliotropioideae* were most thoroughly studied by plant physiologists and phytochemists. This resulted in the detection of several metabolic features which should also interest plant taxonomists. In this respect phenolics, triterpenes and triterpene-based saponins, triglycerides of seeds, carbohydrate storage products and some N-containing compounds other than pyrrolizidines have to be mentioned. Phytochemical reviews of the family are available in Hegnauer (1964, 1989). In the following summary references are usually only given if not available in these two chemotaxonomic treatments.

Boraginoid Pyrrolizidine Alkaloids — These (PAs) belong to the ester-type and are similar to or identical with alkaloids also occurring in *Compositae*–*Eupatorieae* and –*Senecioneae* and in the papilionoid genus *Crotalaria*. Periodical reviews of these often

hepatotoxic alkaloids are published in Natural Products Reports [last review in 11 (1994) 613–619; covers the period July 1992–June 1993]. Another review we owe to Hartmann and Witte (1994). Nowadays much attention is paid to biosynthesis, ecological functions and pharmacology of PAs. Both, the aminoalcohol part, the so-called necines, and the characteristic necic acids of these ester alkaloids derive from amino acids. Moreover, PAs often contain also organic acids other than necic acids. Acetylations occur rather frequently; an example being 7-acetyl-9-latifolylretronecine from *Hackelia californica*. Ehretinine, a PA of *Ehretia aspera*, has replaced the necic acid by 4-methoxybenzoic acid. In plants PAs are often concentrated in the youngest leaves and in flowers and inflorescences. Plant parts with large amounts of PAs are impalatable to many herbivores; PAs form part of the plants defence against herbivory. Some specialists, e.g. many arctiid moths, were able to adapt to this chemical barrier and subsequently evolved means to make use of these toxins for their own defence against potential predators. Larvae of some arctiid moths even transesterify PAs of their host plants to callimorphine or creatonotine, two alkaloids hitherto only known from butterflies feeding on PA-containing plants. Examples are *Gnophaela latipennis* feeding on *Hackelia californica* which contains the already mentioned 7,9-diester of retronecine (L'Empereur et al. 1989) and *Creatonotos transiens* reared on *Gynura scandens* (Compositae–Senecioneae) which has gynuramine, a macrocyclic 7,9-diester of retronecine with an isomer of isatinecic acid, a dihydroxynecic acid with two carboxylic groups, as main alkaloid. *Gnophaela* stores predominantly callimorphine by replacing the necic acid latifolic acid of the PAs of its host plant by 2-acetoxy-2-methylbutanoic acid, and *Creatonotos* stores the monoesters creatonotine and isocreatonotine by replacing the isatinecic acid isomer of gynuramine by 2-hydroxy-3-methylpentanoic acid. The new acids of the butterfly alkaloids generated in the larvae by transesterifications are assumed to be insect metabolites (Hartmann et al. 1990). Both, plants and insects, are able to N-oxidize PAs; N-oxides are main transport and storage forms of these alkaloids. PAs are also present in the nectar of some plants. This feature was interpreted as a mean a plant can use to increase floral constancy of visiting pollinators: generalists are deterred and specialists, e.g. butterflies needing PAs for defence and/or pheromone production (necine-part only), are attracted (Masters 1991).

Alkannin and shikonin and biogenetically related secondary metabolites — Alkannin, a liposoluble red 1,4-naphthoquinone derivative occurs in many *Boraginaceae*. Its biogenesis starts with 3-geranylation of 4-hydroxybenzoic acid and subsequent oxidative decarboxylation yielding C-geranylhydroquinone which has been isolated from wood of *Cordia elaeagnoides*. This key metabolite yields along different routes a whole array of quinonoid and/or phenolic constituents: alkannin-shikonin-like naphthoquinones, arnebifuranone-type 1,4-benzoquinones, the allergic cordiachromones, arnebinol-type phenols, biphenolic shikonofuran-type esters and still other structural variants derivable from geranylhydroquinone. Formerly a tincture made from *Alkanna* roots was used for staining lipids in histochemical work. The lipophilic red pigments known as alkannareds are mixtures of monoesters of alkannin and/or its enantiomer, shikonin. They occur mainly in a number of perennial *Boraginoideae*. Their original sources were roots of

Alkanna tinctoria and roots of *Lithospermum erythrorhizon*. The latter yielded in Japan a crude drug called 'Shikon' (Kariyone-Koiso 1971) or 'Koshikon' to discern it from the imported crude drug 'Nanshikon', which is the dried root of *Macrotomia euchroma* [*Lithospermum euchromon* = *Arnebia euchroma* (Xin-Sheng Yao et al. 1991)]. Alkanna-reds are often produced and stored by plants in roots, but deposition of red pigments is also known from stems and leaves of several species of the American genus *Plagiobothrys*; leaves of *P. arizonica* yielded acetylalkannin. According to recent investigations (Okamoto et al. 1995) biogenesis of shikōnīn in roots of *Lithospermum erythrorhizon* starts with phenylalanin and subsequently yields geranyl-4-hydroxybenzoic acid, geranylhydroquinone and deoxyshikonin. Ultimately shikonin is produced by introduction of a hydroxyl group in the aliphatic side chain; it is this alcoholic hydroxyl which is esterified in the genuine esters of alkannareds or lithospermumreds. Another recent investigation (Ikeda et al. 1991) established the fact that all boraginoid reds are mixtures of esters of the enantiomers alkannin and shikonin; in reds of roots of *Alkanna tinctoria* and *Arnebia euchroma* esters of alkannin dominate (> 95%), and in roots of *Lithospermum erythrorhizon* esters of shikonin are predominant (84–93%). The cordiachromones and closely related compounds were isolated from wood of species of the genus *Cordia*. Microphyllone from *Ehretia microphylla* is probably a derivative of prenylated hydroquinone. A recent investigation of this Philippine medicinal plant resulted in the isolation of the flavonol glycosides astragalin and nicotiflorin, of rosmarinic acid, and of four dimeric monoprenylated *p*-benzoquinones, i.e. microphyllone and three chemically and biosynthetically related compounds; two of the microphyllone-type constituent and rosmarinic acid showed good spasmolytic activity; this perhaps accounts for the use of this plant as antiallergic remedy (Yamamura et al. 1995). The antibiotically active cordiaquinones A to D are C₂₆-compounds which probably derive from farnesylhydroquinone; these compounds were called meroterpenoids, because only part of their structure is of isoprenoid origin (hydroquinone derived from phenylalanin + a sesquiterpenoid unit). In cordiaquinones A, B and D the sesquiterpenoid moiety of the molecules shows an unusual type of rearrangement (Bieber et al. 1990, 1994; Silva Filho et al. 1993). Still another type of compounds generated by this pathway was isolated from the resinous exudate of *Heliotropium filifolium* of arid regions of Chile. This exudate yielded two flavonoids and filifolinol which was shown to be a derivative of a C-geranylated methylester of 4-hydroxybenzoic acid (Torres et al. 1994). Similar compounds seem to occur together with lipophilic flavonoids in *H. stenophyllum* (Urzúa et al. 1993).

Phenolic constituents — Glycosides of the flavonols kaempferol, quercetin and isorhamnetin were reported to be the main flavonoids of *Boraginoideae*, but flavones are not lacking. Apigenin was detected in *Echium simplex*, and *Onosma heterophylla* yielded apigenin, luteolin and chrysoeriol besides quercetin (Mellidis et al. 1993). The 7-glucoside of luteolin was isolated from *Heliotropium tenellum*. Flower anthocyanins are predominantly based on cyanidin, delphinidin and malvidin. Dry leaves of *Cordia verbenacea* yielded the lipophilic exudate flavones artemetin (= 5-hydroxy-3,6,7,3',4'-pentamethoxyflavone) and 6'-hydroxyartemetin. Derivatives of the falvanone hesperetin, of the dihydroflavonol taxifolin and yellow chalcone dimers were isolated from roots, stem-

bark or seeds of several species of *Cordia*. Resinous exudates of *Heliotropium chenopodiaceum* yielded 5 lipophilic flavonoids, i.e. rhamnocitrin, ayanin, and kumatakenin which are methyl ethers of the flavonols kaempferol and quercetin, and the 7,3'-dimethylether of the flavanone eriodictyol, and sakuranetin, the 7-methyl ether of 2,3-dihydrokaempferol; the two exudate flavonoids of *H. filifolium* were identified with galangin, a flavonol with a non-hydroxylated B-ring, and 3-methylgalangin (Urzúa et al. 1993).

Caffeic acid seems to be ubiquitous in the family. It occurs esterified with quinic acid as chlorogenic acids and with α -hydroxydihydrocaffeic acid (formally caffeic acid + H_2O) as rosmarinic acid. Lithospermic acid was isolated from several taxa of *Boraginoideae*; it is a trimeric constituent in which rosmarinic acid is conjugated with a third molecule of caffeic acid by one -C-C- and one -C-O-C-bond, and is therefore a neolignanoid compound containing a benzofuran moiety. *Onosma heterophylla* also yielded an ester of caffeic acid with a 4-phenyl-butan-2-ol derivative and an ester of isoferulic acid with 3-phenylpropan-2-ol (Mellidis et al. 1993). Roots of *Macrotomia euchroma*, an anti-inflammatory Chinese crude drug, yielded two isomeric lignanoid caffeic acid tetramers, one of which proved to be identical with rabdosiin formerly isolated from *Rabdosia japonica* (*Labiatae*; Nishizawa et al. 1990). Rabdosiin and its isomers are rosmarinic acid dimers (or caffeic acid tetramers) present as sodium and potassium salts in roots; these salts were shown to inhibit propagation of human immunodeficiency virus (HIV) (Kashiwada et al. 1995).

Triterpenes and triterpenoid saponins — Free pentacyclic triterpene-monols or their acetates seem to occur frequently. Bauerenol and its acetate, isobauerenol, lupeol, betulin, β -amyrin acetate and α - and β -amyrin were detected in *Ehretia*- and *Symphytum*-taxa (Jaarsma et al. 1989, 1990) and *Sericostoma pauciflorum* (Ayatollahi et al. 1991). Barks of some species of *Ehretia* also yielded betulinic and ursolic acids. Cordialin A and B are multioxygenated tetracyclic dammarane-type triterpenes from leaves of *Cordia verbenacea*. Saponins with triterpenoid sapogenins were isolated from *Anchusa officinalis*, *Caccinia glauca*, *Cordia obliqua*, *Symphytum officinale* (Ahmad et al. 1993; Noorwala et al. 1994; Mohammad et al. 1995) and *Trichodesma africanum* (Omar et al. 1983). Sapogenins were identified with oleanolic acid, hederagenin (= 23-hydroxyoleanolic acid), caccigenin (= 2,19,23-trihydroxyoleanolic acid) and 23-desoxycaccigenin. One of the many saponins of *Anchusa* had 2,19,23-trihydroxyursolic acid as aglycone. The *Cordia*-saponin is based on lupeol and a second *Trichodesma* saponin has β -amyrin as sapogenin. Present knowledge favours the assumption that boraginaceous saponins are mainly based on the pentacyclic oleanolic acid and some of its hydroxylated derivatives. In two instances triterpenic alcohols (β -amyrin, lupeol) replaced triterpenic acids as sapogenins.

Seed oils — Seeds (nutlets) store proteins and fatty oils but lack starch. Seeds of *Boraginoideae* store a specific type of triglycerides characterized by substantial amounts of γ -linolenic acid (18:3, *all-cis* Δ 6,9,12) and of a corresponding tetraenic acid [18:4, *all-cis* Δ 6,9,12,15, called stearidonic acid by Sewón and Tyystjärvi (1993)]. *Cordioideae*, *Ehretioideae* and *Heliotropioideae* seem not to store such seed oils; oleic and linoleic acid are main fatty acids of their triglycerides. Within *Boraginoideae* fatty acid patterns of

seed oils seem to offer taxonomically useful information, e.g. seed oils of *Cynoglossae* and *Anchuseae* additionally contain considerable amounts of 20:1 and 22:1 acids. A new type of seed triglycerides was recently detected in *Trichodesma zeylanicum*; the seed oil of this taxon has a totally different pattern of fatty acids, i.e. 12:0 = 7%, 14:0 = 4%, 16:0 = 21%, 18:0 = 12%, 18:1 = 4%, 18:2 = 14%, ricinoleic (= 12-hydroxyoleic) acid = 22% and 16% of Halphen-positive cyclopropene fatty acids (malvalic and sterculic acids; Hosamani 1994). We do not yet know whether other species of *Trichodesma* produce similar seed oils. It is remarkable that the unusual triglycerides with a high proportion of Δ^6 -trienoic and tetraenoic C_{18} acids are not restricted to seeds; such acids often predominate also in leaf lipids. A recent analysis of the fatty acids of lipids of the edible leaves of *Borago officinalis* showed that they contain mainly palmitic, ordinary linolenic and stearidonic (c. 20% of total) acids and that γ -linolenic acid is present in lesser amounts (1–6% of total acids depending on leaf age) (Sewón & Tyystjärvi 1993).

Carbohydrates including cyclitols — (-)-Bornesitol, a monomethyl ether of myoinositol seems to be present in most species of *Boraginoideae*; it was not yet detected in members of other subfamilies. Scyllitol accompanies bornesitol in several *Boraginoideae* and seems to replace it in a few. Flowers and roots of *Cordia boissieri* yielded pinitol.

Starch and inulin-type fructans are predominant carbohydrate storage products in vegetative plant parts except for annual species. Starch occurs in all four subfamilies and fructans are restricted to *Boraginoideae* where they occur together with starch or totally replace the latter. *Symphytum* belongs to the genera storing starch and fructans in rootstocks, roots and stems; recent detailed fructan investigations were reported for *S. officinale* (Abou-Mandour et al. 1987), *S. palaestinum* (Sitton & Chaouat 1989) and *S. asperum* (Barbakadze et al. 1990).

Allantoin — Probably all *Boraginaceae* contain allantoin in taxon- and plantpart-dependent amounts. This ureide is synthesized by partial degradation of purines. Allantoin is a N-rich metabolite which is used by some taxa of higher plants for temporary storage and for transport of nitrogen. Boraginaceous seeds are often very rich in allantoin.

Miscellaneous compounds — Cyanogenesis occurs erratically in this family. The cyanogenic glucoside dhurrin was isolated from young leaves of *Borago officinalis*. Moreover, making use of reliable tests cyanogenesis was demonstrated for leaves or aerial parts of *Cordia revoluta* (one of two samples), *C. scouleri*, *Heliotropium anderssonii*, *Tournefortia polystachya*, *pubescens* and *rufo-sericea* of the Galapagos Islands and for Australian *Heliotropium amplexicaule* (one of four tested samples).

Another type of nitrile glucosides occurs in roots of several *Lithospermum* taxa: *L. purpureooceruleum* (*Buglossoides purpureooceruleum*). (Sosa et al. 1955; Sosa et al. 1977), *L. ruderale* (Gorman et al. 1956) and *L. officinale* (Sosa et al. 1977). This glucoside was called lithospermoside in 1977. A series of related compounds was isolated from the stem bark of *Ehretia philippinensis* by Simpol et al. (1994): ehretiosides A1, A2 and A3, ehretioside B and simmondsin which was already known from *Simmondsia californica* (*Buxaceae* s.l.). Compare for this strange type of non-cyanogenic cyanoglucosides sub *Caesalpinieaceae* (Flora Malesiana I, 12 (2) 1995: 16). Ehretioside B is the

first lithospermoside-like compound in which the cyclohexene ring is replaced by a fully aromatic ring; this suggests that phenylacetoneitriles derived from amino acids (phenylalanine, tyrosine) may be precursors of simmondsin- and lithospermoside-like plant constituents. Moreover, bark of *E. phillippinensis* yielded rosmarinic acid just as did bark of *E. microphylla* (Simpol et al. 1994).

Prenylation, geranylation and farnesylation of 4-hydroxybenzoic acid and/or hydroquinone is common in the family. It is not surprising therefore that besides such meroterpenoids with hemiterpene, monoterpene and sesquiterpene moieties essential oils containing mainly mono- and sesquiterpenes are produced in appreciable amounts by some members of *Boraginaceae*. Such essential oils were described for the wood of *Cordia chacoensis* and for leaves of *C. cylindrostachya* (Fun & Baerheim Svendsen 1990).

Boraginaceae tend to deposit carbonate of calcium and/or silica in hairs and ordinary epidermis cells. Moreover, it was shown that leaves and nutlets of many members of the family contain an unusual amount of a water-soluble form of SiO_2 . According to Seibert (1978) deposition of large amounts of carbonate of calcium in the peripheral nutlet layers is a character of tribe *Lithospermeae* if some exceptions (the genera *Echium*, *Halacsya* and *Lobostemon* and a few species of *Moltkia* and *Lithodora*) are accepted.

Chemotaxonomy — There are but a few peculiar tendencies of primary and secondary metabolisms which are valid for the family as a whole, i.e. synthesis and storage of the ureide allantoin, of pyrrolizidine alkaloids, and of meroterpenoids based on phenylalanine-derived 4-hydroxybenzoic acid and its oxidative decarboxylation product hydroquinone and a hemi-, mono- or sesquiterpenoid moiety (alkannin, cordiachromones, cordiaquinones and biogenetically related compounds). Perhaps metabolites of caffeic acid, such as dimeric rosmarinic acid, trimeric lithospermic acids and tetrameric rabdosiins are also widespread in *Boraginaceae*; this has, however, only been established for *Boraginoideae* and *Ehretioideae*. Other chemical peculiarities, such as the composition of seed oils, of carbohydrate reserves, accumulation of cyclitols and still other ones appear to be of potential taxonomic use at subfamilial and tribal levels rather than at familiar rank. The position of the family in the system of angiosperms is still somewhat doubtful. In recent time *Boraginaceae* are affiliated to *Solanaceae* rather than to *Labiatae* by some authors. Compare *Solanales-Boraginineae* of Thorne (1992) with *Lamiales* (incl. *Boraginaceae*) of Cronquist (1988). Chemistry of secondary metabolites is not very helpful in this respect. The boraginaceous meroterpenoids confirm the generally accepted strong affinities with *Hydrophyllaceae*, but do not yield unequivocal hints regarding solanaceous or lamiaceous affinities. By rosmarinic acid and the rabdosiins the family is biochemically linked with *Labiatae*, but other metabolic tendencies discussed above and a total lack of iridoid compounds rather favour Thorne's classification.

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USES

Alkannin has been used as a dye in widely distant parts of the world. Species of *Cordia* provide edible fruits and timber. For the latter, South American species have been introduced into culture in Indonesia such as *C. alliodora* and *C. gerascanthus*. Recently, alkannin esters of various organic acids have been introduced into pharmacology for their wound healing properties. *Borago officinalis* is used as a spice.

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TAXONOMY

Delimitation of *Boraginaceae* as a whole is still controversial. While a majority of authors regard them as a natural entity that can further be subdivided into five subfamilies, i.e., *Wellstedioideae*, *Cordioideae*, *Ehretioideae*, *Heliotropioideae* and *Boraginoideae*, others take some of these subfamilies as separate families which are even assigned to different

orders by Hutchinson and his followers. As an example, Takhtajan (1987) may be cited, who excludes the primarily woody *Cordioideae* and *Ehretioideae* as well as the tetrame-rous *Wellstedioideae* from *Boraginaceae* in the strict sense, which are divided into *Heliotropioideae* and *Boraginoideae*. On the other hand, embryologists advocate recognition of a distinct family *Heliotropiaceae* including *Cordioideae* and *Ehretioideae*. There is little doubt that all these groups are closely related to each other. In the present author's opinion, there are no compelling reasons for dividing *Boraginaceae* into several separate families, and they are treated as an entity here.

Boraginoideae are divided into a number of tribes, some of which have been adopted in all newer treatments of the subfamily. These are *Lithospermeae*, *Boragineae* (= *Anchuseae* of older literature), *Eritrichieae* and *Cynoglosseae*. To include some genera ancestral to these tribes and probably closely related among each other, Riedl (1968) adopted an additional tribe originally proposed by Popov (1953) under the name *Trigonotidae*. *Myosotis* is different from all other genera of *Boraginaceae* by its contorted aestivation and is best regarded as the only member of tribe *Myosotidae*.

Synopsis of subfamilies, tribes and genera of *Boraginaceae* represented in Malesia:

Subfamily *Cordioideae*

Trees or shrubs. Fruit a drupe with one quadrilocular or four unilocular pyrenes. Style terminal, twice forked.

In Malesia: *Cordia*.

Subfamily *Ehretioideae*

Trees, shrubs, climbers or rarely herbs. Fruit a drupe with two bilocular or rarely four unilocular pyrenes. Style terminal, simply forked or two styles.

In Malesia: *Carmona*, *Coldenia*, *Ehretia*, *Rotula*.

Subfamily *Heliotropioideae*

Trees, shrubs, subshrubs, climbers, perennial or annual herbs. Fruit with a fleshy, rarely a spongy pericarp and two bilocular or four unilocular pyrenes or hard, usually breaking up into four unilocular nutlets, rarely into two mericarps or not at all. Style terminal, surrounded by the annuliform stigma, entire or forked.

In Malesia: *Heliotropium*, *Tournefortia* (including *Argusia*).

Subfamily *Boraginoideae*

Annual or perennial herbs, rarely subshrubs. Fruit breaking up into four unilocular nutlets, rarely nutlets 1–3 by abortion. Style basifixed between the nutlets and coherent to gynoeceal tissue that is covering the receptacle and separating from the inner layers of the fruit wall, sometimes on top of a pyramidal to subulate gynobasis formed by that gynoeceal tissue, undivided or once to twice forked.

Tribus *Trigonotidae*

Gynobasis flat, slightly concave or slightly convex in its centre. Ventral (inner) side of the nutlets angular, with an open furrow upwards from the subbasal areola at the

angle, or with a simple keel or angle and stipitate areola, or umbilicate ventrally, umbilicus with a thickened margin.

In Malesia: *Bothriospermum*, *Trigonotis*.

Tribus *Boragineae*

Gynobasis flat or nearly flat. Nutlets with a basal areola often surrounded by a thickened margin.

In Malesia: *Borago*.

Tribus *Cynoglosseae*

Gynobasis conical to pyramidate. Nutlets attached for their whole length or only slightly surpassing the gynobasis, free from an early stage.

In Malesia: *Trichodesma*, *Cynoglossum*, *Omphalodes* (?*Crucicaryum*).

Tribus *Myosotideae*

Gynobasis flat, small. Nutlets smooth with a minute subbasal, oblique areola. Corolla-lobes contorted in aestivation.

Only *Myosotis*.

Pteleocarpa is not considered as a member of *Boraginaceae*. It is treated here as a genus of uncertain position at the end of the family.

While there is little doubt that *Boraginaceae* are most closely related to *Hydrophyllaceae* and *Lennoaceae*, their assignment to a particular order is still controversial. Hutchinson (1973) included the woody *Ehretiaceae* in *Verbenales* ancestral to *Verbenaceae*, while *Boraginaceae* s.str. were considered as the only family of a monotypic order *Boraginales* derived from *Polemoniales*.

As has been argued, the woody groups are certainly closely related to the herbaceous ones and should not be placed into a different order. Cronquist (1981) and Thorne (1976) united them with *Labiatae* and *Verbenaceae* in the order *Lamiales*. The alternate leaves, actinomorphic corolla and number of stamens equal to that of corolla lobes along with the presence of pyrrolizidine and not-iridioid alkaloids are strong arguments against this decision as has been pointed out by Dahlgren (1977, 1983) and Thorne (1983), who included the family in *Solanales*, among others. The soundest solution seems to keep *Boraginales* with the families mentioned above as a separate order as proposed by Takhtajan (1980, 1987) and Dahlgren. It is also justified for embryological and anatomical reasons according to Al-Shehbaz (1991). *Boraginales* probably are derived from *Polemoniales* in close vicinity of which they are also placed by Takhtajan (1987).

Literature: Al-Shehbaz, I. A., J. Arnold Arbor., Suppl. Ser. 1 (1991) 1–69. — Brand, A., in: A. Engler, Pflanzenreich, fam. IV.252 (1921) 1–183; *ibid.* (1931) 1–236. — Cronquist, A., An integrated system of classification of flowering plants (1981). — Dahlgren, R. M. T., Publ. Cairo Univ. Herbarium 7/8 (1977) 83–102; Bot. J. Linn. Soc. 80 (1980) 91–124. — Hutchinson, J., The families of flowering plants (1973). — Johnston, I. M., Contr. Gray Herb. 73 (1924) 42–73. — Popov, M. G., in Flora URSS 19 (1953) 97–691. — Riedl, H., in Fl. Iranica 48 (1967) 1–281; Österr. Bot. Zeitschr. 115 (1968) 291–321. — Takhtajan, A., Bot. Rev. 46 (1980) 225–359; Systema magnoliophytorum (1987). — Thorne, R. F., A phylogenetic classification of the Angiospermae, in: K. Hecht et al. (eds.), Evolutionary biology 9 (1976) 35–106; Nordic J. Bot. 3 (1983) 85–117.

KEY TO THE GENERA

- 1a. Style terminal on top of the undivided or divided fruit 2
- b. Style basal between the 4 or rarely fewer separate nutlets. Herbs 9
- 2a. Fruits 2, laterally compressed capsules with a wide wing, bilocular, with one larger erect and one smaller pendent ovule (*Pteleocarpa*, p. 141)
- b. Fruit drupaceous or separating into 4 unilocular nutlets or two 2-locular mericarps, or undivided, hard 3
- 3a. Style once or twice forked, with or without a distinct stigma, sometimes undivided with 2 stigmata. Fruit drupaceous with 1 to 4 pyrenes and 4 seeds 4
- b. Style simple or forked, surrounded by an annular stigma. Fruit drupaceous or separating into 4 nutlets or 2 mericarps 8
- 4a. Style twice forked. Fruit with a single 4-locular pyrene. Trees, shrubs or woody climbers ***Cordia*** (p. 68)
- b. Style simply forked or styles 2. Fruit with two 2-seeded or four 1-seeded pyrenes or remaining entire 5
- 5a. Creeping herb ***Coldenia*** (p. 67)
- b. Trees, shrubs or climbers 6
- 6a. Fruit breaking up into two 2-seeded pyrenes. Style forked ***Ehretia*** (p. 91)
- b. Fruit breaking up into four 1-seeded pyrenes or endocarp remaining entire ... 7
- 7a. Style undivided, with 4 capitate stigmata. Fruit breaking up into four 1-seeded pyrenes. Flowers in a loose, scorpioid inflorescence ***Rotula*** (p. 114)
- b. Style forked to below middle, stigmata indistinct. Endocarp of fruit remaining entire with 4 seeds. Flowers single or a few in fascicles ***Carmona*** (p. 65)
- 8a. Fruit drupaceous. Pericarp corky or fleshy. Trees, shrubs or climbers (in Malesia) ***Tournefortia*** (p. 116)
- b. Fruit separating into 4 nutlets or two 2-seeded mericarps, rarely undivided with mostly 1 locule by abortion ***Heliotropium*** (p. 99)
- 9a. Anthers with long, twisted awns. Fruit separating into nutlets only at a late stage ***Trichodesma*** (p. 124)
- b. Anthers without awns. Fruits with 4 separate locules already at an early stage 10
- 10a. Nutlets perfectly smooth 11
- b. Nutlets warty, with spines, tubercles or glochids 12
- 11a. Nutlets with a ventral keel or angle and a shortly stipitate basal, horizontal areola ***Trigonotis*** (p. 127)
- b. Nutlets without a ventral keel or angle. Areola minute, oblique, not stipitate ***Myosotis*** (p. 109)
- 12a. Filaments with an erect appendix; anthers forming a column, usually subacute. Nutlets with a basal areola surrounded by a thick, tumidulous margin; gynobasis flat ***Borago*** (p. 62)
- b. Filaments without an appendix; anthers not forming a column, obtuse. Nutlets with a subventral areola, gynobasis short conical to pyramidal 13

- 13a. Nutlets without glochids 14
- b. Nutlets flat to convex dorsally, not cup-shaped, with glochids at least marginally and on ventral side 15
- 14a. Nutlets concave dorsally, much larger than 1 mm **Omphalodes** (p. 113)
- b. Nutlets ellipsoidal, scarcely larger than 1 mm **Bothriospermum** (p. 63)
- 15a. Narrowly pyramidal stylar column present between the nutlets **Cynoglossum** (p. 79)
- b. Stylar column absent between the nutlets that are inserted on a flat disc *(Crucicaryum, p. 141)*

BORAGO

Borago L., Sp. Pl. (1753) 137; Gen. Pl., ed. 5 (1754) 172. — Type species: *Borago officinalis* L.

Annual or perennial herbs with long, patent, rigid, bristly hairs in all parts. *Leaves* alternate, lanceolate. *Cymes* many-flowered, bracteate or leafy, combined into a broad, corymb-like structure. *Flowers* on long, spreading or deflexed pedicels, pentamerous. *Calyx* deeply divided, with narrow lobes. *Corolla* with short tube and stellate or campanulate limb, with 5 scales (fornices) in the throat. *Stamens* with long, broad filaments abruptly tapering in their uppermost parts and with an erect, subulate appendage at apex; anthers exerted for the greatest part, laterally coherent, connective produced into a mucro. *Pistil*: style long, filiform. *Nutlets* 4, erect on a flat receptacle, with concave areola.

Distribution — Small genus of 3 species native in the Mediterranean region. *Borago officinalis* is widely cultivated throughout the world.

Notes — 1. The basic chromosome number $x = 8$. There are diploid and tetraploid species.

2. The genus has been treated taxonomically by Gusuleac, Bul. Fac. Stiinte Cernauti 2 (1928) 394.

***Borago officinalis* L.**

Borago officinalis L., Sp. Pl. (1753) 137; Backer & Bakh. f., Fl. Java 2 (1965) 464. — Type: Herb. Cliff. (BM).

Annual, hispid herbs. Stem erect, branched, angular, hollow, 20–120 cm high. *Leaves* alternate, crowded in lower part of stem rosetta-like, lower leaves stalked, petiole 2–8 cm long, upper leaves sessile; blade 3–10 by 2–5(–8) cm, oblong or elliptic, margin entire or sinuate-wavy, obtuse, bristly hairy, nerves especially distinct on lower side, forming a dense network between primary nerves. *Inflorescence* subcorymbose-paniculoid, with few small, lanceolate leaves near base, composed of scorpioid, leafless cymes; pedicels 0.5–2 cm long, patent or recurved. *Calyx* 10–12 mm long, explanate in flower, accrescent to 15–20 mm and forming a tube in fruit, cleft nearly to the base into lanceolate, obtuse lobes with long spreading hairs along margin and on surface.

Corolla 15–25 mm across, blue, tube very short, white, throat with 5 exserted, large fornicies, limb stellately spreading, with oblong-lanceolate to lanceolate, acute lobes. *Stamens*: filaments strongly widening towards base, shorter than anthers, with a spur-like appendix, anthers with an acute apex, 7 mm long, dark violet. *Pistil*: style filiform, stigma capitate. *Nutlets* 5, 7–10 mm long, oblong-ovoid, ventrally keeled, dorsally ribbed, with vertical rows of warts, areola with a white strophiole surrounded by a prominent ring.

Distribution — Of Mediterranean origin, now widely cultivated and sometimes naturalized in Europe, Asia and northern Africa; *Malesia*: Java, cultivated in mountain regions.

BOTHRIOSPERMUM

Bothriospermum Bunge, Enum. Pl. Chin. Bor. (1832) 47. — Type species: *Bothriospermum chinense* Bunge.

Annual or biennial plants. *Leaves* alternate. *Flowers* small, pentamerous, solitary, extra-axillary, forming a kind of leafy raceme in the distal part of the branches. *Calyx* cleft to the base. *Corolla* with scales (fornices) in the throat, with a short tube and spreading limb divided into 5 obtuse lobes. *Stamens* included in the corolla, with short, obtuse anthers. *Pistil*: style short, with small, capitate stigma. *Nutlets* very small, erect, with a tiny areola attached to the flat or nearly flat receptacle, surface usually sculptured, ventral side with a large navel surrounded by a prominent margin.

Distribution — A genus of 5 species with its centre of distribution in China.

Bothriospermum zeylanicum (J. Jacq.) Druce

Bothriospermum zeylanicum (J. Jacq.) Druce, Rep. Bot. Exch. Cl. Brit. Is. 1916 (1917) 610. — *Anchusa zeylanica* J. Jacq., Eclogae 1 (1813) 47, t. 29. — Type: Plate in J. Jacquin, l. c.

Bothriospermum tenellum (Hornem.) Fischer & C. A. Meyer, Index Sem. Hort. Petrop. 1 (1855) 23; C. B. Rob., Philipp. J. Sc., Bot. 4 (1909) 697; Backer & Bakh. f., Fl. Java 2 (1965) 463. — Type in Herb. Vahl (as *Anchusa zeylanica*), 'Hab. in China' (C).

Annual, with numerous stems and subappressed hairs that are only more patent in the petioles and leaf margins. Stems prostrate, 8–25 cm long, slender, simple or nearly simple. Basal leaves soon dry and often vanishing, stem leaves 15–30 by 3–8 mm, decreasing in size upwards, with wavy margin and acute apex, the lower ones stalked, ovate-lanceolate to lanceolate, the upper ones sessile, lanceolate. *Inflorescence* leafy, leaves 7–8 mm by c. 2 mm. *Flowers* not strictly axillary; pedicels 3–5 mm long. *Calyx* c. 2 mm long, with linear-lanceolate lobes. *Corolla* c. 2.5 mm long, salver-shaped, tube shorter than calyx, lobes 5, rounded, explanate; fornicies 5, trapeze-shaped, emarginate at apex. *Pistil*: style short, stigma capitate. *Nutlets* 1–1.2 mm long. — **Fig. 1.**

Distribution — Afghanistan, Pakistan, India, China and adjacent parts of the former URSS, Japan; *Malesia*: Java (naturalized, according to Backer & Bakh. f., l. c.), Philippines.

Habitat — In fields.

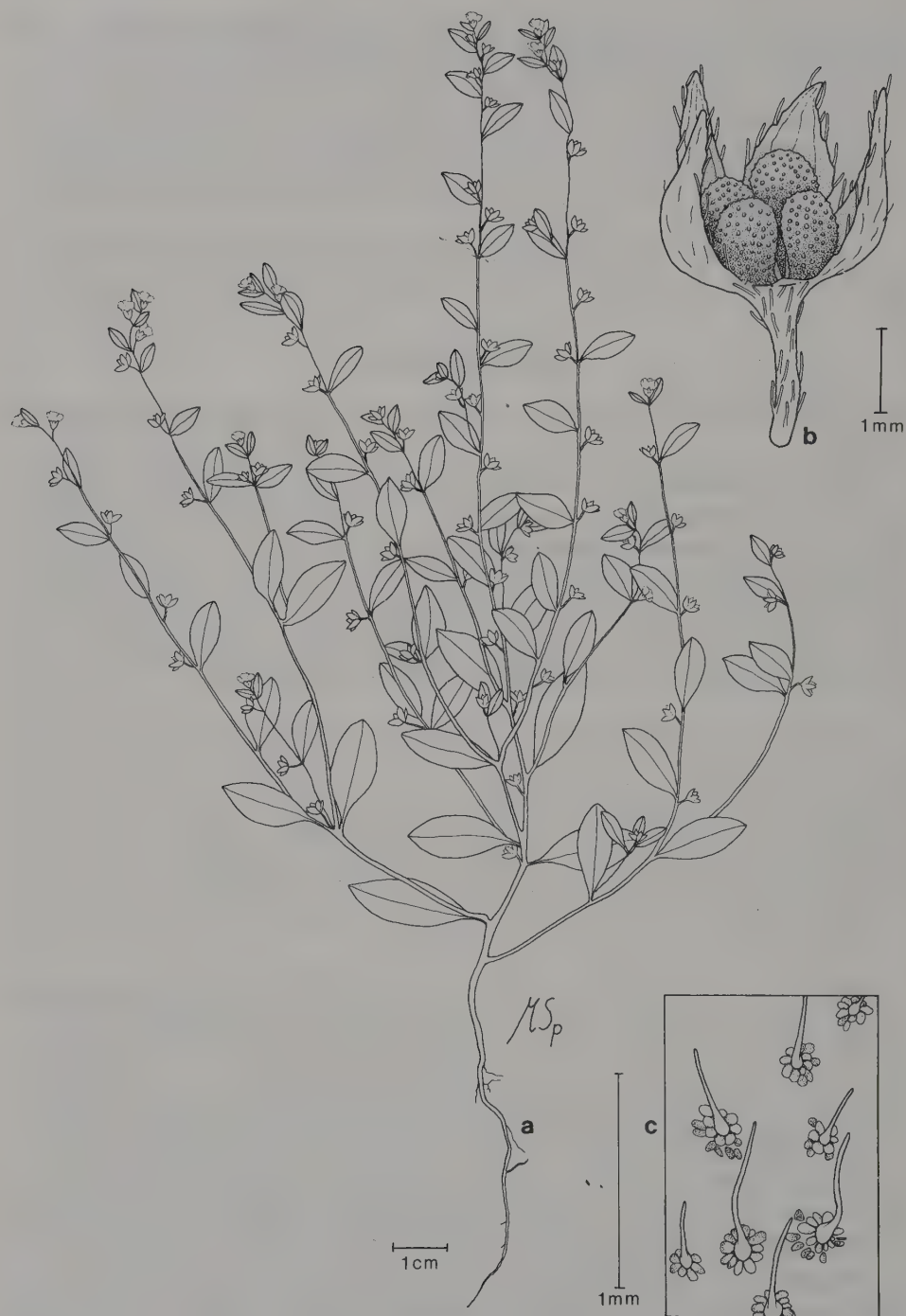


Fig. 1. *Bothriospermum zeylanicum* (J. Jacq.) Druce. a. Habit of plant; b. fruits in calyx; c. upper leaf surface (Backer 21529). Drawing M. Spitteler.

CARMONA

Carmona Cav., Ic. 5 (1799) 22, t. 438; I. M. Johnston, J. Arnold Arbor. 32 (1951) 16; Backer & Bakh. f., Fl. Java 2 (1965) 459; Ng in Tree Fl. Malaya 4 (1989) 59. — Type species: *Carmona heterophylla* Cav. [= *C. retusa* (Vahl) Masamune].

Shrubs or small trees. Branches slender, bearing short shoots with dense clusters of leaves and inflorescences in the leaf-axils. *Leaves* comparatively small, roughly toothed at apex. *Flowers* 2–6 in a short, bractless, glomerulate inflorescence. *Corolla* white, with a short tube and broad, spreading lobes. *Stamens*: anthers exserted. *Ovary*: style terminal, cleft to near base into two slender, elongate arms bearing minute, subcapitate stigmas. *Fruit* globose, drupaceous, red or yellow, with 1–4 seeds, endocarp bony, not breaking up into pyrenes. — **Fig. 2.**

Distribution — A monotypic genus of SE Asia, spreading northwards to southern China, westwards to India, eastwards to New Guinea and the Solomon Islands.

Habitat — Confined to dry places in coastal sands, on rocks, in open woodlands.

Note — *Carmona* has been included in *Ehretia* by most authors prior to Johnston (1951). The most peculiar feature, by which *Carmona* is separated from *Ehretia*, is the undivided, shortly beaked endocarp. Internal cavities are changing in arrangement from base to top. There are 4 large cavities for the seeds extending for the whole length of the endocarp. Near the base of the endocarp they are accompanied by 5 sterile cavities, two large ones on the dorso-ventral line, a small central one and a small cavity to the left and right of both pairs of fertile cavities. At a higher level the number of the last mentioned cavities is increased to 3 on both sides, there are also 2 tiny central cavities between the members of each pair of fertile cavities. In the upper half of the endocarp, the 2 large sterile cavities are replaced by 3, the central tiny cavities are lacking, finally the lateral small sterile cavities are disappearing also below the apex. The number of fertile cavities may be reduced by abortion in rare cases (see also Johnston, l.c.).

Carmona retusa (Vahl) Masam.

Carmona retusa (Vahl) Masam., Trans. Nat. Hist. Soc. Formosa 30 (1940) 61; Backer & Bakh. f., Fl. Java 2 (1965) 459; Ng in Tree Fl. Malaya 4 (1989) 59. — *Cordia retusa* Vahl, Symb. Bot. 2 (1791) 42. — Type: Plukenet, Phytographia, tab. 31, fig. 1 ('Habitat in India Orientali').

Ehretia microphylla Lam., Tabl. Encycl. 1 (1792) 425; C. B. Rob., Philipp. J. Sc., Bot. 4 (1909) 692. — *Carmona microphylla* (Lam.) G. Don, Gen. Syst. 4 (1837) 391; I. M. Johnston, J. Arnold Arbor. 32 (1951) 17. — Type: unknown.

Ehretia buxifolia Roxb., Pl. Corom. 1 (1796) 42; Ridl., Fl. Malay Penins. 2 (1923) 442. — Type: unknown.

Shrub or tree, 1–4(–10) m high, much branched. Juvenile branches hispid, sometimes in addition puberulent, with tomentose buds or short shoots producing clusters of leaves and inflorescences. *Leaves*: petiole 1–5(–10) mm long; blade 0.8–6(–10) by 0.5–2.5(–4) cm, obovate to spatulate, broadest in upper third and gradually narrowing towards petiole, rounded, obtuse or rarely acute, toothed or crenate towards apex, bearing short, rigid, more or less appressed hairs from clusters of mineralized cells. *Inflores-*



Fig. 2. *Carmona retusa* (Vahl) Masam. a. Fruiting twig, most calyces empty; b. fruit in calyx, style broken (Britton 140). Drawing M. Spitteler.

cence: peduncle arising from leaf-axils or apex of short shoots, slender, 0.2–2.5(–4) cm long; flowers 2–6 fascicled or in a scantily branched cyme; pedicels 0–7 mm long. *Calyx* 3–6 mm long, sparsely hispidulous outside, densely hairy inside, lobes linear to linear-spathulate. *Corolla* white, 4.5–6.5 mm long, tube 1.7–2 mm, widening from base upwards, limb 6–9 mm in diam., lobes spreading, 2.5–4.5 mm long. *Stamens*: filaments 2.5–3.5 mm long, the anthers oblong. *Ovary*: style 4.5–6 mm long, bifid, branches 3–5 mm long. *Fruit* globose, 5–6 mm in diam. — **Fig. 2.**

Distribution — India, Sri Lanka, Burma, Thailand, Indo-China, China (Hainan, Kwangtung), Taiwan, Japan (Ryukyu Islands); *Malesia*: Sumatra, Peninsular Malaysia, Java, Philippines, Celebes, Lesser Sunda Islands (Sumba, Flores), Moluccas, New Guinea, Solomon Islands. Often cultivated in gardens for ornamental purposes.

Habitat — Dry regions, sunny forests.

COLDENIA

Coldenia L., Sp. Pl. (1753) 125; Gen. Pl., ed. 5 (1754) 61. — Type species: *Coldenia procumbens* L.

Annual, prostrate herbs with dorsiventrally compressed, ascendingly branched stems. *Leaves* small, crenate-dentate or lobulate, asymmetric. *Flowers* tiny, disposed between the leaves or bracts, neither axillary nor opposed to them, tetramerous. *Corolla* white, with cylindric tube and diminute lobes. *Stamens*: anthers broad, included in the corolla, on 4 short filaments attached to about the middle of the corolla tube. *Ovary* glandular villose, pyramideate; styles terminal, 2, united at base, with tiny stigmas at the apex. *Fruit* rostrate, dividing into two 2-seeded halves first, later halves again divided into single-seeded nutlets; ventral side of nutlets with a sharp angle, dorsal side with corky, vesicular mesocarp; endocarp thick with strong ridges and protuberances.

Note — *Coldenia* was described by Linnaeus as monotypic with the single species *C. procumbens*. In later times, up to as many as 20 American species have been included, until Richardson demonstrated in 1976 that there are marked differences between them and the original *Coldenia*. For the American species, the generic name *Tiquilia* was available. *Tiquilia* species are perennial herbs or subshrubs with symmetric leaves and pentamerous flowers. The endocarp is thin, a mesocarp is entirely lacking.

Literature: Johnston, I.M., Contr. Gray Herb. 70 (1924) 55. — Richardson, A., Sida (Contr. Bot.) 6 (1976) 235; Rhodora 79 (1977) 467.

Coldenia procumbens L.

Coldenia procumbens L., Sp. Pl. (1753) 125; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 693; Ridl., Fl. Malay Penins. 2 (1923) 442; I.M. Johnston, J. Arnold Arbor. 32 (1951) 13; Backer & Bakh. f., Fl. Java 2 (1965) 460. — Type: Plukenet, Phytographia, tab. 64, f. 6.

Stems ascendingly branched, 10–50 cm long, greyish hairy. *Leaves*: petiole 0–5 mm long; blade 5–30 by 3–15 mm, asymmetric, oblong or obovate, crenate-dentate to lobulate, veins 4–6 on each side, impressed above, prominent beneath, strigose between veins, hairs often with bulbous base on upper, spreading on lower surface. *Flowers* subsessile. *Calyx* 1.5 mm long, slightly accrescent in fruit, lobes 4, lanceolate or ovate-lanceolate. *Corolla* white, glabrous, 1.5–1.8 mm long, tube 1–1.3 mm long, lobes ascending, 0.2–0.4 mm long, rounded. *Stamens*: filaments inserted above middle of corolla, included, longer than the anthers. *Ovary* glandular-villose; style bifid nearly to the base. *Fruit* 3–4 mm long, pyramidal, 4-lobed, nutlets beaked, strongly convex by vesicular, corky mesocarp dorsally, sharply angulate ventrally, with one large and one small commissural face. — **Fig. 3.**

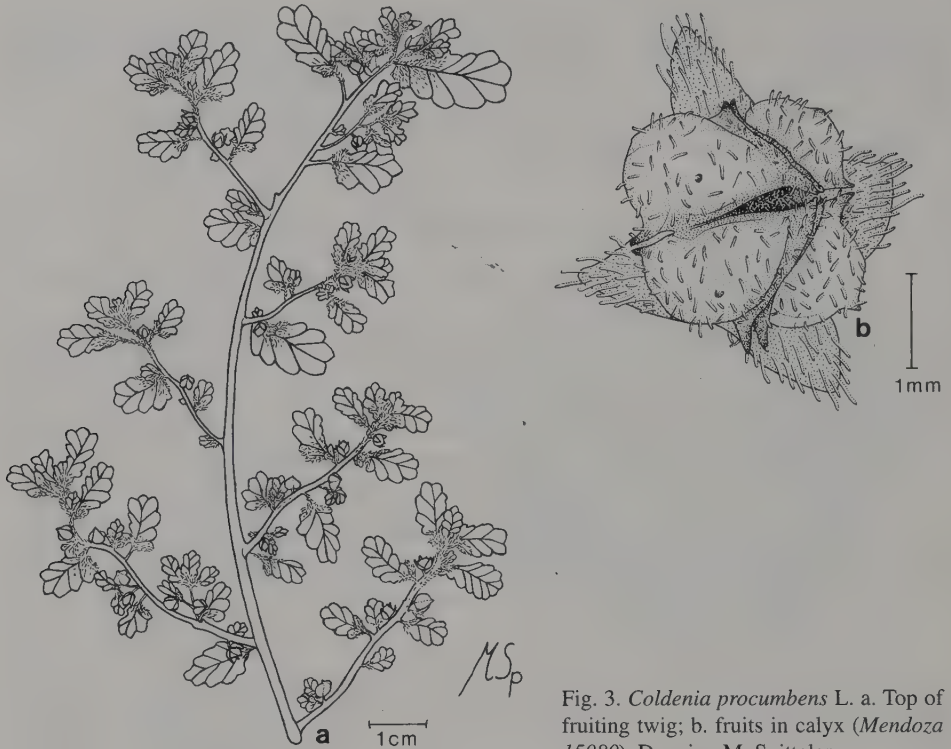


Fig. 3. *Coldenia procumbens* L. a. Top of fruiting twig; b. fruits in calyx (Mendoza 15080). Drawing M. Spitteler.

Distribution — India, Sri Lanka, Thailand, Burma, Indochina, China (Hainan), Taiwan; *Malesia*: Malay Peninsula, Borneo, Java (incl. Madura), Lesser Sunda Islands (Flores, Timor), Moluccas, New Guinea. Widespread in tropical and subtropical SE Asia, Africa and Australia.

Habitat — On desiccating land subject to seasonal floodings, rice-fields, etc.

Ecology — A plant of seasonally flooded places, but also able to stand extreme heat and drought. It is a common weed in dry rice-fields. The corky mesocarp may be useful for dispersal in ponds and ditches.

CORDIA

Cordia L., Sp. Pl. (1753) 190; Gen. Pl., ed. 5 (1754) 87; I.M. Johnston, J. Arnold Arbor. 32 (1951) 2; Heine in Fl. Nouv.-Caléd. 7 (1976) 97; Borhidi et al., Acta Bot. Hung. 34 (1988) 375–423; Ng in Tree Fl. Malaya 4 (1988) 60; Heubl et al., Bot. Jahrb. Syst. 112 (1990) 129. — Type species: *Cordia sebestena* L.

Medium sized trees, shrubs or woody climbers. *Leaves* alternate, rarely subopposite, stalked, usually entire, sometimes indistinctly crenate. *Inflorescences* terminal or axillary, paniced to corymbose, sometimes very few-flowered, subglobose, with scorpioid branches. *Flowers* with a short, distinct pedicel or sessile, (4–)5–16-merous, bisex-

ual, sometimes functionally monosexual and dioecious. In male flowers the ovary reduced and style absent, in female flowers the anthers sterile. *Calyx* cup-shaped to campanulate or tubular, lobes either irregular, 3–12, or regular, 5, or very short and reduced to a membranous, irregular margin, in some species growing with the mature fruit and becoming fleshy. *Corolla* hypocrateriform or funnel-shaped, large or small; lobes imbricate or nearly contorted in bud. *Stamens* of same number as corolla-lobes, included or exserted; filaments glabrous or pubescent at base; anthers oblong, ovate to subquadrate. *Ovary* 4-locular with one erect ovule in each locule; style twice forked, terminal; stigma elongate on each branch or subcapitate. *Fruit* drupaceous, as a rule partially included in the persistent, cupuliform calyx. *Pollen grains* 3-colpate, 3-colporate or 3-colporoidate, sexine tectate to semi-ectate, striate-reticulate or spiny and tuberculate in the Malesian species, 3-porate to pantoporate with semitectate, reticulate sexine bearing microtubercles in the exclusively American subgenus *Varronia*. — **Fig. 4.**

Distribution — A pantropical genus of about 250–300 species. In *Malesia* represented by 8 indigenous species and 4 species introduced from tropical America.

Morphology and anatomy — Certain anatomical features seem to be of taxonomic value. Crystals present in the secondary xylem can either be described as crystal sand, or there are prismatic crystals either additionally or as the only type, or a special columnar type of crystals is developed. As far as known, only *C. subcordata* is characterized by crystal druses.

In the leaves, cystoliths either are confined to epidermal cells or also found in the basal part of trichomes.

Hairs, especially of the axis, are simply strigillose or with two horizontal, apical branches, or they are stellate (especially in subg. *Gerascanthus*), sometimes, especially in American groups, bearing glandular heads.

Chromosome numbers are derived from the basic numbers 7 (in subg. *Myxa*), 8 (in subg. *Cordia* and in some species of subg. *Gerascanthus*), 9 (in subg. *Varronia*) and 15 (in some species of subg. *Gerascanthus*). Polyploidy is not infrequent. The highest diploid number counted is 'more than 80' in *C. rothii* (subg. *Myxa*).

Literature: Gottwald, H., IAWA Bull., new ser. 4 (1983) 161. — Heubl, G.R. et al., Bot. Jahrb. 112 (1990) 129. — Mez, C.C., Bot. Jahrb. 12 (1890) 526.

Uses — Some *Cordia* species are cultivated for their timber. Medicinal use is mentioned for *C. dichotoma* and *C. 'myxa'* (Jansen et al. 1991).

Reference: Jansen, P.C.M., et al. (eds.), Plant Resources of South-East Asia (PROSEA). Basic List (1991) 227.

Taxonomy — The delimitation of the genus *Cordia* has varied a great deal in the past from author to author. It has been split into as many as ten different genera (Friesen 1933), while I.M. Johnston (1930 to 1951) accepted it in a broad sense dividing it into 5 sections. The most recent treatment by Borhidi et al. (1988) takes an intermediate path acknowledging three genera: *Cordia*, *Varronia* and *Gerascanthus*. *Cordia* is not subdivided any further, in the exclusively American genus *Varronia* three sections are recog-

nized, in *Gerascanthus* two subgenera. Unfortunately, the very thorough morphological, anatomical and cytological paper of Heubl et al. (1990) was not yet known to them. Taking into account obvious correlations in chromosome numbers, pollen morphology and crystal pattern in the wood among each other and with other characters, it seems better to include *Gerascanthus* in *Cordia* and ascribe generic rank to the much more different *Varronia*, as has been proposed already by De Candolle in 1845. In the Malesian area, only true *Cordia* is found according to that proposal. It is further divided into three subgenera in the following way.

Cordia* L. subg. *Cordia

Cordia L. subg. *Cordia*. — *Sebesten* [Dill. ex] Adans., Fam. Pl. — *Cordia* L. sect. *Sebestenoides* DC., Prodr. 9 (1845) 476.

Large flowered. Fruit with corky mesocarp, completely enclosed by the calyx. Pollen 3-colpate to 3-colporoidate, exine striate-reticulate. In the secondary xylem and pith, columnar crystals (united to druses in *C. subcordata*) present along with crystal sand. $x = 8$.

In Malesia only *C. subcordata*.

***Cordia* L. subg. *Cerascanthus* (P. Browne) Cham.**

Cordia L. subg. *Gerascanthus* (P. Browne) Cham., Linnaea 5 (1831) 115. — *Gerascanthus* P. Browne, Civ. Nat. Hist. Jamaica (1756) 170. — *Cerdana* Ruiz & Pavon, Prodr. (1794) 37. — *Cordiada* Vellozo, Fl. Flumin. (1829) 98. — *Cordia* sect. *Cerdanae* (Ruiz & Pavon) Roem. & Schult., Syst. 4 (1818) 499.

Small flowered. Fruit single-seeded with a thin, fibrous, chartaceous carpel-wall, at the mature state surrounded by the cylindrical calyx and the tube of the marcescent corolla. Pollen 3-colpate or 3-colporoidate, exine spinulose. Secondary xylem with medium-sized crystals often in groups of 2–8. $x = 8$ or 15.

Exclusively American, but some species (*C. alliodora*, *C. gerascanthus*) also cultivated in SE Asia.

***Cordia* L. subg. *Myxa* (Endl.) Taroda**

Cordia L. subg. *Myxa* (Endl.) Taroda, Rev. Bras. Bot. 9 (1986) 38. — *Collococcus* P. Browne, Civ. Nat. Hist. Jamaica (1756) 167. — *Cordia* sect. *Myxa* Endl., Gen. Plant. (1840) 644. — *Cordia* sect. *Pilicordia* A.DC. in DC., Prodr. 9 (1845) 474. — *Calyptracordia* Britton, Sci. Surv. Porto Rico 6 (1925) 122. — *Myxa* (Endl.) Friesen, Bull. Soc. Bot. Genève 24 (1933) 136.

Small flowered, flowers often dimorphic. Fruit with a watery or viscid endocarp, frequently dispersed by birds or mammals. Pollen 3-colpate to 3-colporate, exine finely spinulose to verrucose. Usually, only crystal sand present in the secondary xylem, but rarely also prismatic crystals. $x = 7$.

References: Johnston, I.M., Contr. Gray Herbarium 92 (1930) 1; J. Arnold Arbor. 21 (1940) 336; ibid. 30 (1949) 85; ibid. 31 (1950) 172; ibid. 32 (1951) 1, 99. — Friesen, F.C.V., Bull. Soc. Bot. Genève II, 24 (1933) 117. — Borhidi, A., et al., Acta Bot. Hung. 34 (1988) 375. — Heubl, G.R., et al., Bot. Jahrb. 112 (1990) 129.

KEY TO THE SPECIES

- 1a. Inflorescence a simple, unbranched cyme **5. *C. curassavica***
- b. Inflorescence branched in various ways 2
- 2a. All the herbaceous parts covered by stellate, appressed and longer, simple, patent hairs. Inflorescence paniculate **1. *C. alliodora***
- b. Stellate hairs absent. Inflorescence more or less corymbose, rarely paniculate . . . 3
- 3a. Corolla 2–4 cm long. Calyx cylindrical 4
- b. Corolla shorter than 2 cm. Calyx never cylindrical 5
- 4a. Inflorescence paniculate. Leaves more than 3 times as long as wide, lanceolate . . .
..... **7. *C. gerascanthus***
- b. Inflorescence more or less corymbose. Leaves ovate, acute, usually less than twice
as long as wide **9. *C. subcordata***
- 5a. Leaves glabrous to nearly glabrous except along nerves on lower side. 6
- b. Leaves hairy, at least on the whole lower side 7
- 6a. Fruit 20–30 mm long. Calyx glabrous, campanulate **4. *C. cochinchinensis***
- b. Fruit up to 15 mm long. Calyx hairy to glabrescent, cup-shaped **6. *C. dichotoma***
- 7a. Leaves coriaceous, upper side glabrous, lower side tomentose with hairs brown
when dry **3. *C. bantamensis***
- b. Leaves not markedly coriaceous, upper side hairy at least at a younger stage, lower
side with hairs of various types. 8
- 8a. Leaves green on both sides. Hairs reddish brown in all parts. Inflorescence always
terminal **2. *C. aspera***
- b. Leaves much paler on the lower side. Hairs whitish to greyish, leaving calcareous
tubercles on the upper side. Inflorescence terminal or axillary **8. *C. monoica***

1. *Cordia alliodora* (Ruiz & Pavon) Oken

Cordia alliodora (Ruiz & Pavon) Oken, Allgem. Naturgesch. 2 (1841) 1098. [≡] *Cerdana alliodora* Ruiz & Pavon, Fl. Peruv. II (1799) 47, t. 184. — *Gerascanthus alliodorus* (Ruiz & Pavon) Borhidi, Acta Bot. Hung. 34 (1988) 396. — Type: Ruiz & Pavon s.n. (MA holo; F), Peru.

Tree up to 20 m high, with grey, fissured bark. All herbaceous parts densely covered by very short, stellate hairs, especially the inflorescence. *Leaves*: petiole 1–3 cm long; blade broadly elliptic, 10–55 by 5–25(–30) cm, base obliquely truncate, subacute, apex subacute to acuminate, coriaceous, margin entire, upper surface glabrous, with slightly impressed nerves, lower surface stellate-pubescent with prominent nerves. *Inflorescence* terminal, laxly branched, with numerous, crowded flowers. *Calyx* subglobose, greyish pubescent, with 10 prominent ribs, 6–7(–14) mm long, truncate with indistinct teeth. *Corolla* tube longer than calyx, lobes oblong, rounded, 5–10 by c. 3 mm. *Fruit* 5 mm long, c. 3 mm in diam., deciduous together with calyx and corolla.

Distribution — Native in Central and South America south to Bolivia, north to Mexico, and in the West Indies. *Malesia*: in Sabah (Distr. Sandakan) introduced as a plantation tree.

Ecology — Remarkable for its myrmecophily; swellings are formed on branches and sometimes also in inflorescences, which serve as domatia for ants. Ants use to cut the leaves into small pieces.

2. *Cordia aspera* G. Forst.

Cordia aspera G. Forst., Fl. Ins. Austr. (1786) 18, nr. 109. — Type: 'Tongatabu' in herb. Forster (BM holo).

Cordia cumingiana Vidal, Phan. Cuming. Philipp. (1885) 187; C. B. Rob., Philipp. J. Sc., Bot. 4 (1909) 689. — Types: *Cuming* 1012, 1647, 1653, no lectotype selected.

Cordia propinqua Merr., Philipp. Govt. Lab. Bur. Bull. 35 (1906) 60. — Type: unknown.

Small tree or scrambling shrub. Young branches with a greenish brown bark and dense, patent, bristly hairs. *Leaves*: petiole 0.7–8 cm long; blade ovate-acute, (2.5–)5–22 by 1.5–16 cm, margin finely serrate with cuspidate teeth, base obliquely to subhorizontally truncate or rounded, apex acute to acuminate, rarely subobtusate, nerves (3–)4–6 on each side, darker upper surface short strigillose, pale lower surface tomentose. *Inflorescence* subcorymbose, lateral, subterminal or in fork of uppermost branches; peduncle 0.7–3.5 cm long. *Flowers* numerous; pedicels less than 1 mm long. *Calyx* subcylindrical to cylindrical-campanulate, with 10 distinct, longitudinal ribs, 3–3.5 mm long, 2–2.5 mm wide in flower, widened to 3.5(–4) mm in fruit, with 5 distinct, triangular, acute lobes, reddish tomentose. *Corolla* 3 mm long, tube cylindrical, lobes revolute, 2 mm long, scarcely 1 mm wide, oblong. *Stamens* with short filaments, anthers exserted from the corolla. *Fruit* ovoid, acute, (5–)8 by (4–)5 mm.

Distribution — Solomon, Tonga, Fiji, Samoa Islands, New Caledonia, Australia; *Malesia*: Borneo, Philippines, Celebes, Lesser Sunda Islands (Sumbawa, Flores, Timor), Moluccas, New Guinea.

Habitat & Ecology — No data available.

Note — One of the most characteristic qualities of this species are the 10 well marked ribs of the calyx. This is also one of the main reasons to include *C. cumingiana* Vidal in *C. aspera*.

KEY TO THE SUBSPECIES

- 1a. Leaves ovate to suborbicular-acuminate, 10–12 cm long. Fruit only 5(–6) mm long, 4 mm wide **b. subsp. microcarpa**
- b. Leaves markedly longer than wide, up to 22 cm long. Fruit 8 mm long, 5 mm wide 2
- 2a. Leaves very loosely strigillose to glabrescent on upper, loosely tomentose on lower side, acuminate. Calyx in flower 4 mm in diameter, campanulate to cup-shaped **c. subsp. miquelii**
- b. Leaves densely strigillose on upper, densely tomentose on lower side, acute. Calyx in flower subcylindrical, not more than 3.5 mm in diameter **a. subsp. aspera**

a. subsp. aspera

Leaves up to 22 mm long, markedly longer than wide, ovate, acute, densely tomentose on lower surface. Number of flowers in inflorescence very great. Flowering calyx subcylindrical, fruiting calyx obconical. Fruit 8 mm long.

Distribution — Solomon, Tonga, Fiji, Samoa Islands, New Caledonia, Australia; *Malesia*: Borneo, Philippines, Moluccas, New Guinea.

b. subsp. microcarpa Riedl

Cordia aspera G. Forst. subsp. *microcarpa* Riedl, Blumea 38 (1994) 461. — Type: *Verheijen 4495* (L. holo), Flores.

Leaves 10–12 mm long, ovate to suborbicular, acuminate; hairs as in subsp. *aspera*. Fruiting calyx flat cup-shaped to nearly saucer-shaped, c. 5 mm in diam. Fruit 5(–6) by 4 mm.

Distribution — *Malesia*: Lesser Sunda Islands (Sumbawa, Flores, Timor)

c. subsp. miquelii Riedl

Cordia aspera G. Forst. subsp. *miquelii* Riedl, Blumea 38 (1994) 461. — *Cordia miquelii* Meijer Drees, nomen in herb. L. — Type: *Koorders 16283/3* (L. holo), Celebes, Minahasa.

Leaves up to 15(–20) cm long, distinctly longer than wide, ovate to oblong-acuminate, apart from young ones much less densely tomentose on the lower surface than the typical subspecies. Flowering calyx campanulate to cup-shaped, with revolute lobes after flowering. Inflorescence composed of a much smaller number of flowers than in the typical subspecies, with often thickened branchlets. Fruit c. 8 mm long.

Distribution — *Malesia*: Celebes.

3. *Cordia bantamensis* Blume

Cordia bantamensis Blume, Bijdr. (1826) 843; Backer & Bakh. f., Fl. Java 2 (1965) 459. — Type: *Blume s.n.* (L. holo), Java, Tjikandje.

Cordia calocoma Miq., Fl. Ind. Bat. 2 (1856) 916. — Type: *Horsfield s.n.* from Java, Surakarta.

Tree or climber, 3–10 m high. Branches with a grey to tawny bark, tomentose while still herbaceous. *Leaves*: petiole 1.2–6 cm long; blade elliptical to ovate, 7–22 by 4–12 cm, margin entire to wavy, base rounded-decurrent to rounded or subcordate, apex obtuse to acuminate, nerves 4 or 5 on each side, darker than surroundings when dry on lower surface, glabrous on the upper, tomentose on the lower surface. *Inflorescence* paniculoid, with 10–12 flowers subcapitate at end of (up to 5) branches, axillary, on a 2–3 cm long peduncle; pedicels 1–3 mm long. *Calyx* campanulate, 6–7 mm long, c. 4 mm wide in flower, broadly cup-shaped, 8–9 mm long and up to 15 mm wide in fruit, tomentose, with 5 triangular lobes in flower, that become broadly triangular to indistinct in fruit. *Corolla* cylindrical with reflexed lobes, tube shorter than calyx, transverse diam-

eter c. 7 mm, lobes broadly rounded, c. 4 mm long. *Stamens* with short filaments, included in the corolla. *Fruit* ovoid, rostrate, 15–18 by c. 10 mm.

Distribution — *Malesia*: Sumatra, Java, Lesser Sunda Islands (Bali, Flores, Timor).

Habitat & Ecology — Periodically dry areas, brushwoods, sunny forest (Backer & Bakhuizen f., l.c.).

Note — On Timor, leaves are often comparatively narrow for their length and show fine white, calcareous dots under a lens similar to *C. dichotoma*.

4. *Cordia cochinchinensis* Gagnep.

Cordia cochinchinensis Gagnep. in Fl. Indo-Chine 4 (1914) 203. — Type: *Pierre 413* (P lecto), Bavia, Cochinchina.

Cordia premnifolia Ridl., J. Roy. As. Soc. Straits Br. 68 (1915) 12; Fl. Malay Penins. 2 (1923) 439. — Type: unknown.

Tree, 10–12 m high, or scrambling shrub. Branches soon lignescent, first dark reddish brown, later pale yellowish to greyish brown, glabrous. *Leaves*: petiole 1.5–4 cm long; blades of two kinds: those more distant from apex of branches often broader, 9–12 cm long, w/l ratio about 2/3 to 3/4, with 5 nerves on each side, the rest 5–11 cm long, up to half as wide as long, with c. 8 nerves on each side, all with entire margin, base rounded to transversely truncate or subcordate, apex acute to acuminate, nerves forming a dense network on lower side, glabrous on the upper, with few hairs along the primary nerves on the lower side. *Inflorescence* dichotomously branched, cymes with 2 to 5 flowers, terminal, rarely lateral on short branches; pedicels 1–2 mm long. *Calyx* 3 mm long and wide immediately after flowering, 8–10 mm long, 10–15 mm wide in fruit. *Corolla* (according to Gagnepain) elongate, 15 mm long, tube 8 mm, straight, often broadening towards base round the ovary, lobes 4, ovate-lanceolate, 3 mm long, recurved. *Stamens* 4; filaments exserted. *Fruit* ovoid, up to 3 cm long, 22 mm in diam., tapering towards apex.

Distribution — Cambodia, Vietnam, Thailand; *Malesia*: Peninsular Malaysia.

Habitat & Ecology — No data available.

5. *Cordia curassavica* (Jacq.) Roem. & Schult.

Cordia curassavica (Jacq.) Roem. & Schult., Syst. Veg. 4 (1819) 460. — *Varronia curassavica* Jacq., Enum. (1760) 14; Sel. Stirp. (1763) 40. — Type from Curaçao.

Cordia cylindristachya auct. florae Malaysiae non (Ruiz & Pavon) Roem. & Schult.: Corner, Wayside Trees (1940) 176; Ng in Tree Fl. Malaya 4 (1989) 60.

Shrub, c. 1–4 m high. Young branches rough hispidulous, becoming reddish brown. *Leaves*: petiole 5–6 mm long, blade 3–10(–15) by 2–4(–5) cm, lanceolate to ovate-lanceolate, margin serrate, tapering and acute at both ends, glabrous to sparsely hispid and with tiny white tubercles on upper side, paler and soft pubescent beneath. *Inflorescence* unbranched, spike-like scorpioid, developing basipetally, terminal, 5–15(–25) cm long. *Calyx* sessile, 3–4(–5) mm long, finely pubescent or papillose, lobes triangular,

1.5 mm long. *Corolla* tubular, 4–5 mm long, white, with small, reflexed lobes 2 mm long and wide. *Fruit* globose, 5 mm in diam., hidden in the calyx.

Distribution — Central America, Antilles, northern South America. In *Malesia* introduced in W Malaysia, Singapore and Borneo at the end of last century.

Habitat & Ecology — No data available.

Note — All Malesian specimens examined clearly belong to *C. curassavica*. This species is distinct from *C. cylindristachya*, under which name it is found in the herbaria and cited in literature, by narrower leaves that are never velvety or tomentose but rough, exclusively terminal, often longer inflorescences and smaller calyces and corollas. The hairs on the calyx are much shorter than those in *C. cylindristachya*.

6. *Cordia dichotoma* G. Forst.

Cordia dichotoma G. Forst., Fl. Ins. Austr. (1786) 18, nr. 110; I.M. Johnston, J. Arnold Arbor. 32 (1951) 8; Backer & Bakh. f., Fl. Java 2 (1965) 459; Ng in Tree Fl. Malaya 4 (1989) 60, excl. syn.

Cordia suaveolens Blume; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 98, f. 2. — Type: *Forster s.n.*, New Caledonia.

Cordia blancoi Vidal, Rev. Pl. Vasc. Filip. (1886) 192; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 688. — Type: not extant, neotype never selected.

Cordia myxa auct. non L.: Koord., Exk. Fl. Java 3 (1912) 127; Merr., Fl. Manila (1912) 393.

Cordia obliqua auct. non Willd.: Koord., Exk. Fl. Java 3 (1912) 127; Ridl., Fl. Malay Penins. 2 (1923) 439.

Cordia subdentata Miq., Sumatra (1860) 571. — Type: *Diepenhorst s.n.* from W Sumatra.

Cordia griffithii C.B. Clarke in Hook. f., Fl. Brit. India 4 (1885) 139; Ridl., Fl. Malay Penins. 2 (1923) 439. — Type: *Griffith s.n.*, Malacca.

Tree or shrub, 6–20(–27) m high. Younger branches grey, greyish brown to brownish, glabrous. *Leaves*: petiole 1–4.5 cm long; blade ovate, ovate-lanceolate, broadly ovate, rarely suborbicular, 2–12(–16 in sterile branches) by 1.2–10 cm, margin entire, wavy, sometimes crenulate towards apex, papyraceous to coriaceous, base rounded-decurrent to oblique truncate to subcordate, apex acute, acuminate, obtuse to rounded, nerves (3–)4–5 on each side, prominent below, mostly small whitish, flat groups of mineralized cells in 2 circles on upper, sparsely hairy or with more numerous hairs along nerves on lower side. *Inflorescence* subcorymbose to subthyrsoid, with pseudo-dichotomous branching, terminal on slender lateral branches with 2–4 leaves, rarely lateral, with a highly variable number of flowers. *Calyx* cup-shaped, expanded in fruit from a narrow base, 3–5 mm long, slightly accrescent in fruit, 3–4 mm wide in flower, 6–10 mm in fruit, with short, dense hairs in flower, later glabrescent, lobes shortly triangular, reflexed. *Corolla* cylindrical-campanulate, white, 5–6(–8) mm long, tube 3 mm, limb 5 mm in diam., lobes 5, oblong, reflexed, 2 by 1 mm. *Stamens* long exserted. *Fruit* ovoid, c. 10(–15) mm long, c. 8(–10) mm in transverse diam. — **Fig. 4.**

Distribution — New Caledonia; *Malesia*: Sumatra, Peninsular Malaysia, Singapore, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands (Bali, Lombok, Sumbawa, Flores, Alor, Timor), Moluccas, New Guinea.

Habitat — Mainly at low altitudes from sea level upwards to about 500 m, an aberrant specimen from New Guinea also on mountain top in sunny position.

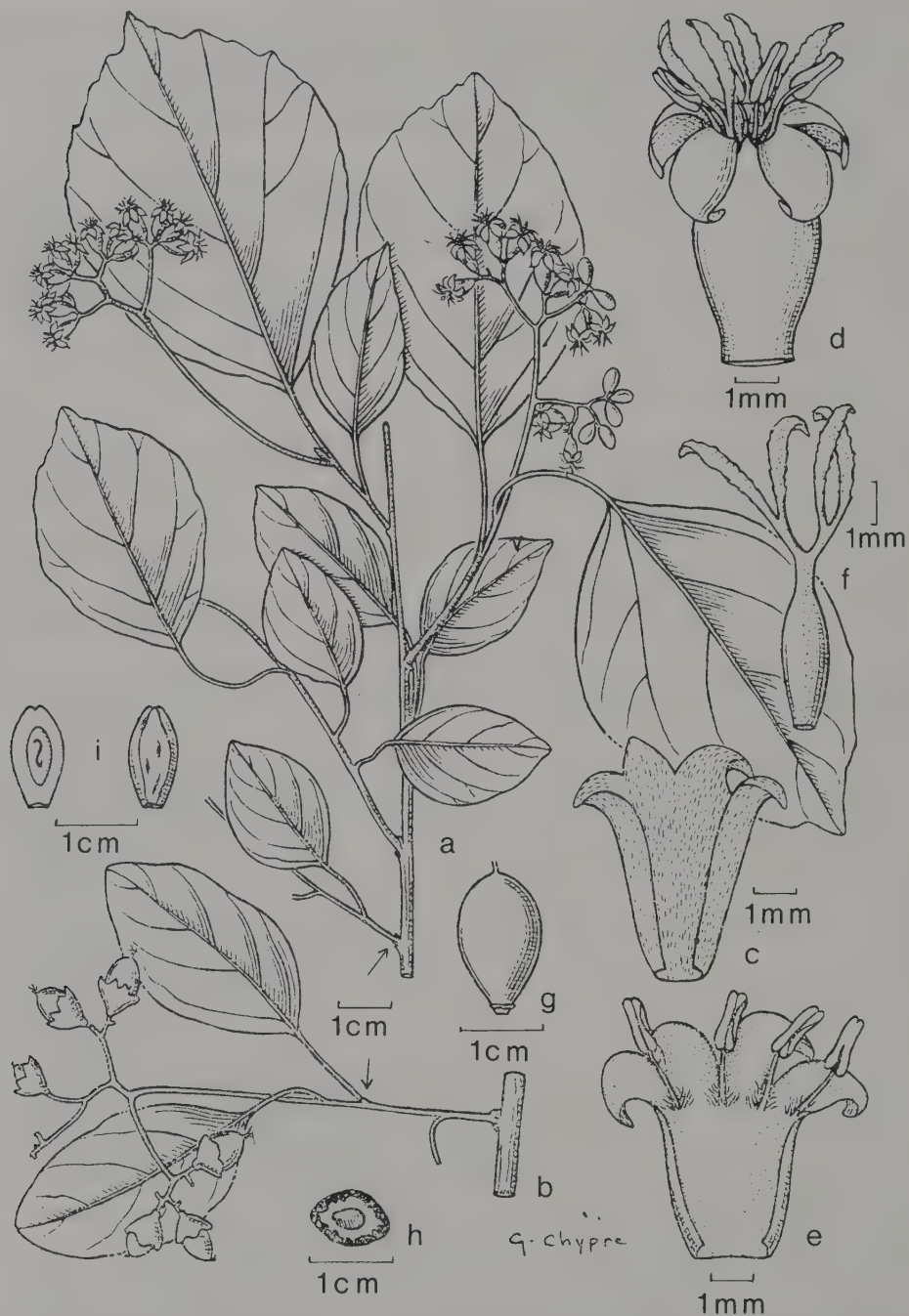


Fig. 4. *Cordia dichotoma* G. Forst. a. Flowering twig; b. fruiting twig; c. calyx; d. corolla with stamens and styles; e. opened corolla with stamens; f. pistil; g. fruit; h. fruit, cross section; i. endocarp (left) with length section (a, c–f *Catala* 7458, b, g–i *MacKee* 13770). Drawing G. Chypre. Reproduced with permission from Fl. Nouvelle-Calédonie 7.

Notes — 1. In general, variability of this extremely polymorphic species increases from West to East. In the Philippines, leaves are usually strictly flat and entire at the margin. On New Guinea, there are also species with very large (long and broad), entire leaves.

2. Especially unusual collections include: *Vera Santos 4707* (Philippines, Cagayan du Sulu, Mt Kamutyajan) with ovate, grossly dentate, leathery leaves, flowers 8 mm long, calyx 6 mm long, 6–7 mm wide already in flower; *Gebo UPNG 234* (New Guinea, Central Province, Port Moresby District, on mountain summit) with dark brown twigs, broadly ovate to suborbicular, grossly dentate leaves, calyx c. 4 mm long, corollas included in calyx.

7. *Cordia gerascanthus* L.

Cordia gerascanthus L., Syst. Veg., ed. 10 (1759) 936. — Type: P. Browne, Civ. Nat. Hist. Jamaica (1756) t. 19, f. 3.

Tree, 10–15(–30) m high. Branches glabrous. *Leaves*: petiole 1.5–2.5 cm; blade lanceolate, lanceolate-ovate or elliptic-oblong, 5–12 by 1.5–4 cm, margin entire, base acute, apex acute to acuminate, glabrous on both sides. *Inflorescence* paniculoid, composed of dense, much branched cymes. *Calyx* sessile, tubular, 7–10 mm long, with 10 distinct longitudinal ribs, sparsely hirsute with short hairs or glabrescent, lobes 5, deltoid. *Corolla* funnel-shaped, 15–25 mm long, white, becoming lavender and, when getting dry, brown, tube cylindrical, as long as calyx, lobes obovate, apically truncate to retuse. *Stamens* exserted, filaments inserted below throat, pubescent, woolly at base, anthers sagittate. *Ovary*: style deeply bifid. *Fruit* enclosed by persistent corolla and calyx.

Distribution — Mexico, Central America, West Indies, Colombia. In *Malesia* introduced in cultivation in the Philippines.

8. *Cordia monoica* Roxb.

Cordia monoica Roxb., Pl. Corom. 1 (1796) 43, t. 58; Backer & Bakh. f., Fl. Java 2 (1965) 458.

In *Malesia* one of the subspecies (but see note 2).

subsp. *subpubescens* (Decne.) Riedl

Cordia monoica Roxb. subsp. *subpubescens* (Decne.) Riedl, Blumea 38 (1994) 461. — *Cordia subpubescens* Decne., Herb. Timor. 67; Nouv. Ann. Mus. Hist. Nat. III, 3 (1834) 395, t. 16–21; Miq., Fl. Ind. Bat. 2 (1856) 918. — Type: *Guichenot 322, bois no. 41* (P lecto), Timor.

? *Cordia trichostemon* DC., Prodr. 9 (1845) 482; Miq., Fl. Ind. Bat. 2 (1856) 916. — Type: *Exp. Baudin* (P), Timor.

Cordia leucocoma Miq., Fl. Ind. Bat. 2 (1856) 917. — Type: *Teijsmann s.n.*, Java, Besuki.

Tree, 5–10 m high. Younger branches reddish brown, with few longer, patent, flexuous hairs and brownish or white pubescence, older ones brownish, glabrescent. *Leaves*: petiole (2–)5–30 mm; blade broadly ovate to suborbicular or oblong-ovate, (0.8–)1.5–10 by (0.7–)1–6.5 cm, margin irregularly crenate to grossly dentate, sometimes undu-

late, base rounded, truncate to subcordate, rarely decurrent into petiole, apex acute, acuminate or broadly rounded, with 3–5 nerves on each side, short dense hairs and longer hairs arising from groups of mineralized cells on upper side (denser in what has been called *Cordia leucocoma*), either equally distributed soft, longer hairs or hairs confined to nerves on lower side. *Inflorescence* corymbose to paniculoid, from 2.5 cm in lateral to 12 cm in terminal position wide, with a very large number of flowers; pedicels 1–3 cm long. *Calyx* campanulate, 4 mm long, 3 mm wide in flower, broadly cup-shaped, 4 mm long, 6–7 mm wide in fruit, lobes 3–5, broadly triangular, brownish or whitish pubescent. *Corolla* salver-shaped, with cylindrical tube and explanate to reflexed lobes, white, 3.5–4.5 mm long, c. 5 mm in diam., lobes obovate-spathulate, 2.5 by 1.5 mm. *Stamens*: filaments slightly exserted from the tube. *Fruit* broadly ovoid, rostrate, 6 mm long, 5 mm in diam.

Distribution — *Malesia*: Java, Kangean Archipelago, Lesser Sunda Islands (Bali, Sumbawa, Flores, Timor).

Notes — 1. Subsp. *subpubescens* is different from subsp. *monoica* (India, Sri Lanka) by its short, more or less appressed pubescence combined with longer, patent hairs on branches (subsp. *monoica* has stiff, patent, shorter and longer hairs). The pyrenes are 9–12 mm long in subsp. *monoica*.

2. Plants with only white pubescence on branches and dense hairs with larger groups of mineralized cells on upper surface of leaves have been called *Cordia leucocoma*. They may represent a separate variety.

9. *Cordia subcordata* Lam.

Cordia subcordata Lam., Tabl. Encycl. 1 (1792) 421; Miq., Fl. Ind. Bat. 2 (1856) 914; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 689; Ridl., Fl. Malay Penins. 2 (1923) 439; I.M. Johnston, J. Arnold Arbor. 3 (1951) 3; Ng in Tree Fl. Malaya 4 (1989) 62; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 100. — Type: *Commerson s.n.* (P-JU), 'ex insulis Praliniis'.

Cordia moluccana Roxb., Fl. Ind., ed. Carey & Wall., 2 (1824) 337; Miq., Fl. Ind. Bat. 2 (1856) 916. — Type: not indicated.

Cordia rumphii Blume, Bijdr. (1826) 843. — Type: ?*Blume s.n.* from W Java.

Cordia banalo Blanco, Fl. Filip. (1837) 124. — Type: not extant.

Tree, 2–15 m high. Branches grey to light brown, wood orange. *Leaves* with a 2–8 cm long petiole; blade ovate to elliptic, 8–20 by 5–15 cm, entire or rarely with few teeth, base obtuse to rounded, rarely subcordate, apex obtuse to rounded, rarely acute and shortly acuminate, with 4–5(–6) primary nerves on each side, upper surface slightly nitidulous, with very short, appressed hairs, sometimes with small groups of mineralized cells at base of hairs, lower surface velutinous or even tomentose along median and primary nerves. *Inflorescence* terminal, composed of 6–20 flowers, with a short peduncle. *Calyx* cylindrical, 10–20 mm long, 4–8 mm wide, glabrous or with few short, rigid hairs, with 3 short, triangular lobes, persistent, strongly accrescent and envelopping the fruit. *Corolla* 3.5–5 cm long and wide, orange, the lobes 5–7, large, rounded-truncate. *Stamens*: filaments inserted above middle and at base of limb of corolla, exserted. *Fruit* obovoid to subglobose, 20–30 mm long, 15–25 mm in diam.

Distribution — E coast of Africa, India, Cambodia, Vietnam, Pacific Islands; *Malaysia*: Borneo, Java, Philippines, Celebes, Kangean Islands, Lesser Sunda Islands (Sumbawa, Flores, Alor, Timor), Moluccas, New Guinea

Habitat — Sandy or gravelly beach, beach forests.

Vernacular name — Salimolé (Java).

EXCLUDED OR DOUBTFUL NAMES

Cordia ? dubiosa Blume, Bijdr. (1826) 844.

Note — According to Koorders, Exk. Fl. Java 3 (1912) 127, who had examined the very incomplete type specimen at Leiden, it belongs to a species of *Elaeocarpus*, probably *E. floribunda*.

Cordia olitoria Blanco, Fl. Filip. (1837) 123.

Note — According to Blanco's notes to the description, the species is characterized mainly by its greenish white leaves. The name is not mentioned in later publications, and not even Merrill tried to identify it with any known species.

CYNOGLOSSUM

Cynoglossum L., Sp. Pl. (1753) 134; Gen. Pl., ed. 5 (1754) 168; Brand in Engl., Pflanzenr., fam. IV. 252 (1921) 114; Popov in Fl. URSS 19 (1953) 657; Riedl, Österr. Bot. Z. 109 (1962) 385; Backer & Bakh. f., Fl. Java 2 (1965) 463; Riedl in Fl. Iran. 81 (1967) 142. — Type species: *Cynoglossum officinale* L.

Paracynoglossum Popov in Fl. URSS 19 (1953) 717; R.R. Mill, Notes Roy. Bot. Gard. Edinb. 41 (1984) 473.

Annual, biennial or perennial herbs with alternate, entire *leaves*; basal leaves usually already withered at flowering time. *Cymes* with or without bracts, terminal and axillary, terminal ones often in pairs. *Flowers* extra-axillary, pentamerous, on longer or shorter, but nearly always distinct pedicels. *Calyx* divided beyond middle, often nearly to the base. *Corolla* cylindrical, campanulate, funnel-shaped or rotate, white, blue or purple, sometimes white with blue or purple veins, with 5 distinct scales in the throat. *Stamens* always inserted below the scales, included in the corolla, with very short filaments and short, ellipsoidal, rounded anthers. *Pistil*: style long or short, with or without a distinct stigma, sometimes nearly hidden between the nutlets. *Nutlets* 4, attached to the conical receptacle by an areola that is markedly shorter than the inner side of the nutlet, sometimes additionally with an awn; outer (ventral) side sometimes surrounded by a tumidulous margin or the widening, joined bases of the innermost series of marginal glochids, concave, flat or convex, often less densely covered by glochids than the rest of the nutlet, or not different at all. — **Fig. 5.**

Distribution — 50 to 60 species in the warmer and temperate regions of all continents.

Habitat — The species of this genus display a great variety of habitat preferences.

Uses — *Cynoglossum amabile* Stapf from southern China is used as an ornamental plant in many areas, e.g. most parts of Europe, Indonesia, etc.

Notes — 1. The basic chromosome number is $x = 12$ with most species being diploid, only a few tetraploid.

2. Delimitation of the genus has become controversial in recent years. While the European and N African *Pardoglossum* Barbier & Mathez and the Australian *Austrocynoglossum* R. Mill are very natural groups clearly different from true *Cynoglossum*, *Paracynoglossum* Popov is hard to separate even on the subgeneric level. The main distinguishing character, presence of an awn united with the receptacle and separating from it at maturity of the nutlets in *Cynoglossum* s.str., is not always recognizable. The only other difference, smaller nutlets and often also corollas in *Paracynoglossum*, is working only on a statistical basis, and there are intermediates such as *C. microglochin* Benth. The present author prefers to retain *Paracynoglossum* for the time being on a subgeneric level, though a final decision is still impossible. Especially African species like *C. coeruleum* Hochst. or *C. johnstonii* Bak. assigned to sect. *Eleutherostylum* by Brand are very closely related to typical members of *Paracynoglossum* and have been transferred to it by Mill.

In the Malesian region, the genus is represented by the two subgenera *Paracynoglossum* and *Eleutherostylum*.

Cynoglossum L. subg. *Paracynoglossum* (Popov) Riedl

Cynoglossum L. subg. *Paracynoglossum* (Popov) Riedl, Österr. Bot. Z. 109 (1962) 392.

Nutlets connected to receptacle or style by an awn. Nutlets small, usually not longer than 3–3.5 mm, but with few exceptions up to 4.5 mm. Style usually much longer than nutlets.

The Malesian species *C. furcatum*, *hellwigii*, *javanicum*, *lanceolatum*, *timorense*, and probably also *C. amabilis* belong to this subgenus.

Cynoglossum L. subg. *Eleutherostylum* Brand

Cynoglossum L. subg. *Eleutherostylum* Brand in Engl., Pflanzenr. fam. IV.252 (1921) 115, 140.

Nutlets not connected to receptacle or style by an awn. Nutlets usually bigger, 4 mm or longer. Receptacle distinctly surpassed by the apex of the nutlets, style often very short.

KEY TO THE SPECIES

- 1a. Branches of inflorescence crowded at apex, at acute angles. Leaves greyish-white, velvety **1. *C. amabile***
- b. Branches of inflorescence at different levels, often furcate at apex. Hairs of leaves different 2

- 2a. Corolla broadly cylindrical, up to 10 mm long. Nutlets 6 mm in diam., with a distinct margin **11. C. papuanum**
- b. Corolla campanulate, funnel-shaped or rotate, shorter. Nutlets rarely up to 6 mm 3
- 3a. Corolla with a short tube and a wide, rotate limb c. 8–10 mm in diam. Leaves glabrescent, with mineralized pustules at a later state. Calyx-lobes glabrous on their outer surface **5. C. glabellum**
- b. Corolla either of different shape and size or leaves markedly hairy, not glabrescent. Calyx-lobes hairy on outer surface 4
- 4a. Nutlets 5(–6) mm long. Robust plant at least 75 cm high **2. C. castaneum**
- b. Nutlets smaller 5
- 5a. Corolla c. 12 mm in transverse diam. Plant 50–75 cm high. Nutlets c. 4–4.5 mm long **10. C. novoguineense**
- b. Corolla (and usually the whole plant) smaller. Nutlets 1.5–4.5 mm long 6
- 6a. Whole plant golden silky-tomentose. Corolla white **3. C. celebicum**
- b. Plant with different kind of hairs. Corolla blue to dark purple at least in part . . 7
- 7a. Style distinctly shorter than nutlets. Nutlets with very short, few, slender, subulate spines, attached to the receptacle with a very small, apical areola. Lobes of corolla 3.5 mm long and wide **9. C. macrolimbe**
- b. Style longer than nutlets. Nutlets with longer and usually more numerous glochids. Attachment to receptacle different. Corolla lobes smaller 8
- 8a. Lowermost pedicel 1–1.5 cm long, recurved. Inflorescence few-flowered, flowers remote. Flowers and nutlets very small **13. C. spec. A**
- b. Pedicels fairly equal or the lowermost pedicel a little longer, but not as much as 10 mm. Flowers more or less dense 9
- 9a. Nutlets c. 1.5–2.2 mm long, with short pedicels or nearly sessile **8. C. lanceolatum**
- b. Nutlets 2.5–3(–3.5) mm long, with longer or short, distinct pedicels 10
- 10a. Fruiting cymes spreading, rigid, uppermost forked, lower ones subhorizontal 11
- b. Fruiting cymes not spreading nor rigid, at least uppermost at acute angles, sub-erect 12
- 11a. Corolla campanulate to funnel-shaped, up to 3 mm long. Nutlets 2–3 mm long . . **6. C. hellwigii**
- b. Corolla campanulate, up to 5 mm long. Nutlets 3–4 mm long **4. C. furcatum**
- 12a. Pedicels filiform, recurved, longer than calyx. Nutlets c. 2–2.5 mm long **12. C. timorense**
- b. Pedicels stouter, recurved or patent, not longer than calyx. Nutlets 3(–3.5) mm long **7. C. javanicum**

1. *Cynoglossum amabile* Stapf & Drumm.

Cynoglossum amabile Stapf & Drumm., Kew Bull. (1906) 202; Backer & Bakh. f., Fl. Java 2 (1965) 463. — Syntypes: *Hancock 133, Henry 9365, Soulié 861, Pratt 887* (K), China.

Perennial herbs, 15–60 cm high. Stems single, rarely several, erect, with dense, spreading hairs. *Leaves* velvety, greyish white, with distinct nerves on lower side, basal ones with a long petiole, 5–20 cm long, 2–3.5(–4) cm wide, oblong-lanceolate to lanceolate, acute at the apex, tapering into petiole; cauline leaves sessile with broad, rounded base, oblong to lanceolate, (2–)3–10 by up to 2.5 cm. Lowest *cymes* in the axils of upper leaves, upper ones crowded, at acute angles, erect, ebracteate; pedicels 2–3 mm long in flower, elongated to c. 4 mm and curved downwards in fruit. *Calyx* 2.5–3.5 mm long, greyish pubescent, lobes ovate, acutish, free to base. *Corolla* blue, rarely white, 5–6 mm long; tube c. 2.5 mm long, limb spreading, 7–10 mm in diam.; fornicies papillate, trapeziform. *Stamens*: anthers subsessile between fornicies, 1 mm long. *Pistil*: style twice as long as nutlets. *Nutlets* whitish, ovate in outline, 3–4 mm long, dorsally slightly concave to slightly convex, covered equally by glochids all over, the marginal glochids confluent at the base, nearly forming a wing; areola above middle of ventral surface.

Distribution — A native of southern China, now widely cultivated; *Malesia*: cultivated in Java.

2. *Cynoglossum castaneum* Riedl

Cynoglossum castaneum Riedl, Blumea 38 (1994) 462. — Type: *Afriastini 488* (BO, K), Central Java, Mt Lawu.

Biennial or perennial herb (base unknown), at least 75 cm high. Stem with several elongate branches, covered with short, appressed, usually retrorse hairs. Basal *leaves* not known, stem leaves sessile, acute, linear-lanceolate, covered by short, strigillose, antrorse hairs on the upper, by similar, irregularly directed hairs on the lower side, nerves more or less distinct on lower side only, middle ones 10–12 cm long, 1.5 cm wide, tapering towards base, upper ones 2.5–5.5 cm long, 0.5–1.5 cm wide, semiamplexicaulous. *Cymes* elongate after flower, ebracteate; pedicels 1.5 mm long in flower (at top of cyme), up to 5 mm in fruit (near base). *Calyx* 2.5 mm long in flower, 3(–3.5) mm in fruit, strigillose with antrorse hairs, lobes free to base, ovate, up to 2 mm wide, subacute. *Corolla* funnel- to salver-shaped, with bluish veins on whitish ground, 3.5–4 mm long, 7 mm in diam., tube about as long as calyx, lobes oblong-obovate, rounded, c. 2 mm long, glabrous; fornicies sub-trapeziform to sub-quadrate, involute and emarginate at apex. *Stamens*: anthers ovoid or ellipsoid, 1 mm long, subsessile. *Pistil*: style 0.8 mm in flower, c. 2.5 mm in fruit, without distinct stigma. *Nutlets* ovate in outline, shining castaneous brown, glochids dense and confluent at base at margins, more or less evenly distributed on dorsal and ventral surfaces, areola small, subapical.

Distribution — *Malesia*: Central Java. Known only from the type collection.

Habitat — No data available.

3. *Cynoglossum celebicum* Brand

Cynoglossum celebicum Brand in Engl., Pflanzenr., fam. IV.252 (1921) 147. — Type: *Sarasin 1289* (B, destroyed), Celebes.

Biennial or perennial (base not known). Whole plant golden sericeous tomentose. Stem more than 40 cm high, upright, angulate, branched in the upper part. Basal leaves unknown; stem leaves tapering gradually into a short petiole or semiamplexicaulous, lanceolate-oblong to oblong, 15–20 cm long with petiole, 1.2–4.5 mm wide, slightly attenuate at apex. *Cymes* terminal and axillary, dense, ebracteate, on long peduncles; flowers subsessile, fruiting pedicels very short, slightly bent downwards. *Calyx* 3.5 mm long, sepals free to the base. *Corolla* white, cylindrical-campanulate, 4 mm long, lobes ovate, as long as tube; fornicies subquadrate. *Stamens*: anthers subsessile in the middle of the tube. *Pistil*: style very short, but much longer than the nutlets. Immature nutlets only known, very small, rounded, with very short glochids, inserted at base of the elongated gynobase.

Distribution — *Malesia*: Celebes. Known only from the type collection.

Note — The description is taken from the original diagnosis.

4. *Cynoglossum furcatum* Wall.

Cynoglossum furcatum Wall. in Roxb., Fl. Ind., ed. Carey & Wall., 2 (1824) 6; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 696. — Type: Described from a plant in the Botanical Garden, Calcutta, native in Nepal.

Cynoglossum zeylanicum Brand in Engl., Pflanzenr., fam. IV.252 (1921) 134, p.p., non Thunb. ex Lehm. (1817), nomen in syn. = *Echinosperrum zeylanicum* Lehm.

Biennial or perennial. Stems up to 1 m or more high, with numerous branches especially in the upper part, covered by soft, more or less appressed hairs. Stem leaves sessile, lanceolate or ovate-lanceolate or lanceolate-oblong, lower and middle ones 7–8 by 2.5–3 cm, upper ones 1.5–4 by 0.8–1.5 cm, all gradually tapering towards base, sometimes semiamplexicaulous, acute, with very distinct nerves and with soft, appressed, more or less distinctly retrorse hairs densest along the nerves on both sides. *Cymes* terminal on main stem and lateral branches, mostly paired, divaricate, densely scorpioid in the beginning, straight in fruit, ebracteate; pedicels 1–3 mm long, bent downwards after flowering, covered with very dense, antrorse hairs. *Calyx* c. 2.5 mm long in flower, lobes 2 mm long, 1 mm wide in flower, 4.5–5 by 2(–2.5) mm in fruit, very densely covered by antrorse hairs. *Corolla* campanulate, blue, 4–5 mm long, 5–7 mm in diam., glabrous, tube shorter than calyx, lobes suborbicular, c. 2 mm in diam.; fornicies subquadrate, large. *Stamens*: anthers subsessile, much smaller than fornicies, inserted below them. *Pistil*: style c. 2 mm long in fruit (without gynobase), stigma small, like a helmet on top of the style. *Nutlets* ovate in outline, 3–4 mm long, c. 2.5 mm wide, dorsally slightly convex, with glochids fairly equally distributed all over the surface.

Distribution — Afghanistan, Pakistan, Himalayas, India, China, Japan; *Malesia*: Java, Philippines.

Habitat — No data available.

5. *Cynoglossum glabellum* Riedl

Cynoglossum glabellum Riedl, Blumea 38 (1994) 462. — Type: *Veldkamp & Stevens 5554* (L. holo), New Guinea, Mt Suckling.

Perennial; rhizome divided into creeping branches. Stems several, ascendent, 40–45 cm high, unbranched or with a single branch, glabrous below, strigose with short retrorse hairs in the inflorescence. Apart from the stems there are sterile rosettes of leaves. *Leaves* lanceolate to lanceolate-oblong, acute, on the upper side with numerous, on the lower side with a few groups of mineralized cells very rarely bearing short hairs, ciliate in the margins; leaves of basal rosettes stalked, petiole 3–5 cm long, lamina 5–7 by 1–1.8 cm; lower stem leaves already dry at flowering time, middle ones 3–6 by 0.7–1.4 cm with narrowing base, upper ones 1.8–3 by 0.7–1 cm. *Inflorescence* bifurcate with erect branches or simple, loose, 1.5–8 cm long, composed of only 7–11 flowers, ebracteate; pedicels 4–6 mm long, recurved in fruit. *Calyx* 2 mm long in flower, 4 mm in fruit, crispulate hairy at the very base, lobes 1.3 mm wide in flower, up to 2 mm wide in fruit, subobtusate, with reticulate veins, ciliate at margins. *Corolla* mauve in bud, then deep blue, salver-shaped, 4–5 mm long, 8–9 mm in diam., glabrous, tube about as long as calyx or a little shorter, lobes obovate, 3–3.5 mm long, with reticulate veins; fornications quadrate, emarginate, papillate at margin. *Stamens*: filaments distinct, 0.2 mm long, anthers oblong to ovate-oblong, 0.8 mm long, inserted below fornications. *Pistil*: style 2.5 mm long in fruit, without stigma. *Nutlets* ovate in outline, 4–4.5 mm long, 2.5 mm wide, with dense glochids ventrally and at margin and loosely arranged glochids on the flat dorsal disc.

Distribution — *Malesia*: New Guinea, known from two collections.

Habitat — On dry and rocky flats or on treefern grassland, usually along rivers.

Note — A very distinct endemic species without any close relatives.

6. *Cynoglossum hellwigii* Brand

Cynoglossum hellwigii Brand in Fedde, Repert. 13 (1915) 546. — Type: *Hellwig 362* (B, destroyed), New Guinea, Finisterre Mts.

Cynoglossum javanicum auct. non Thunb. ex Lehm.: Van Royen, Pac. Sc. 29 (1975) 95; Alpine Fl. New Guinea 4 (1983) 3123.

Annual or biennial herb. Stem 8–100 cm high, branched very much, hirsute with dense, more or less distinctly retrorse hairs in the lower, antrorse hairs in the upper part of stem and branches. *Leaves* elliptical oblong, oblong, elliptical, oblong-lanceolate or lanceolate; petiole 4–7 cm long in lower leaves, gradually decreasing in length upwards; blade 12–15 by 3.5–5 cm, long tapering towards petiole in lower leaves, 7–10 by 1–3 cm in middle, 1.5–6 by 0.3–1.5 cm, sessile with narrow base in upper leaves, obtuse to subacute, with numerous, very distinct nerves on both sides, strigose with antrorse longer and shorter hairs, the longer ones arising from groups of mineralized cells on upper, with soft, spreading hairs denser along the nerves on lower side. *Inflorescence* much branched, cymes divaricate, ebracteate; pedicels less than 1 mm in flower, 1–3 mm in fruit, patent or curved downwards, densely hairy. *Calyx* 1.5–2 mm long in

flower, lobes 2.5 mm long, 0.8–1 mm wide in fruit, obtuse, hairs subappressed, antrorse. *Corolla* white or pale blue, campanulate to funnel-shaped, glabrous, 2.5–3 mm long, 3.5–4 mm in diam., tube slightly shorter or equal to calyx, lobes oblong, 1.5–1.8 mm long, 1–1.2 mm wide; fornicies large, subquadrate. *Stamens*: filaments very short, anthers ovate, half the size of the fornicies, reaching their bases. *Pistil*: style 1.5 mm long, stigma small, bilobed. *Nutlets* ovate in outline, convex dorsally, 2–3 mm long, 1.5–2 mm wide, glochids equally distributed or slightly looser dorsally.

Distribution — *Malesia*: New Guinea, widespread, endemic.

Habitat — Swampy grassland along river, open places, 1200–1300 m altitude.

Vernacular name — Mai Rokh.

Uses — Used locally for adornment of wigs.

7. *Cynoglossum javanicum* Lehm.

Cynoglossum javanicum Thunb. ex Lehm., Neue Schr. Naturf. Ges. Halle 3 (1817) 21; Pl. Asperif. (1818) 118, in syn.; Backer & Bakh. f., Fl. Java 2 (1965) 463; Van Royen, Pac. Sc. 29 (1975) 95, p. min. p.; Alpine Fl. New Guinea 4 (1983) 3123, p. min. p. — Type: *Herb. Thunberg*, Java.

Biennial (?) herb. Stem 30–100 cm high, branched, with antrorse to patent hairs arising from groups of mineralized cells. *Leaves* oblong to ovate-oblong or oblong-lanceolate or lanceolate, petiole 1–1.5 cm long in lower leaves, absent in upper, blade up to 12 cm long, (0.7–)1–2.5(–3) cm wide in lower, 4–9 by 0.5–2.5 cm in middle, 2–4 by 0.25–2 cm in upper leaves, tapering towards petiole, in uppermost leaves sessile with narrow or broad base, acute, more rarely obtuse, nerves distinct on both sides, hairs antrorse, arising from a group of mineralized cells on upper, antrorse, denser along nerves on lower side. *Inflorescence* terminal on main stem and lateral branches, cymes more or less upright, at sharp angles, ebracteate, sometimes with a single leaf above lowermost flower; pedicels 1 mm in flower, 2.5–3(–5) mm in fruit, curved downwards. *Calyx* 1.5–2 mm long in flower, lobes ovate, 2.5 mm long, 1.2 mm wide in fruit, obtuse, rounded at apex, with antrorse hairs. *Corolla* dilute blue or pink, campanulate to funnel-shaped, 3–4(–5) mm long, c. 6 mm in diam., lobes suborbicular, 1.5–2 mm by 2 mm, papillate on inner side; fornicies trapeziform, large, as long as wide, sometimes slightly bilobed, involute and papillate at upper margin. *Stamens*: filaments very short, anthers oblong, below fornicies. *Pistil*: style 1–1.5 mm long, stigma indistinct. *Nutlets* broadly ovate in outline, 3 mm long and wide, glochids equally distributed, conical, sometimes bases of marginal glochids widened, confluent. — **Fig. 5.**

Distribution — *Malesia*: Sumatra, Java, ?Bali, ?Lombok.

Habitat — *Casuarina* forests, waste fields (acc. to Backer & Bakhuizen f., l.c.).

Notes — 1. Specimens from the Tengger Mts, E Java, have remarkably narrow leaves and small nutlets with a distinct rim formed by the bases of marginal glochids. Specimens from Bali and Lombok (only one seen from each) are very untypical with more patent, rough indument and may represent a local subspecies.

2. There are plants that have a general habit intermediate between *C. javanicum* and *C. lanceolatum*, between *C. javanicum* and *C. furcatum* as well as between *C. javani-*



Fig. 5. *Cynoglossum javanicum* Lehm. a. Top of plant in flower and fruit; b. fruit with detail of barbed spine (d); c. fruiting calyx, nutlets fallen (*Danser 6585*). Drawing M. Spitteler; a. adapted from an old drawing in L.

cum and *C. timorense*. The delimitation of the species is still far from clear, and it may prove necessary to divide it into several subspecies, as geographical correlations seem to exist in many cases, or even into several species. On the other hand, *C. timorense* and *C. hellwigii* may prove as mere subspecies, though at the moment the differences seem to be constant.

8. *Cynoglossum lanceolatum* Forssk.

Cynoglossum lanceolatum Forssk., Fl. Aegypt.-Arab. (1775) 41; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 94. — Type: Forsskål (C), Yemen, Hadie.

Cynoglossum micranthum Desf., Tabl. Ec. Bot. (1804) 220; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 696. — Type: Hb. Forsskål 312 (C).

Biennial (?) herb. Stems up to 100(–150) cm high, much branched, with longer, patent and shorter, antrorse hairs. *Leaves* lanceolate or oblong-lanceolate, petiole 1.5–3 cm long in lower, 0–1 cm in upper leaves, blade up to 10–11 by 3–3.5 cm in lower, 5–9 by 1.3–1.8 cm in middle, 1.5–6 by 0.3–1 cm in upper leaves, tapering towards base, acute, nerves very distinctly impressed on upper, prominent on lower side, upper side strigose with hairs arising from groups of mineralized cells, hairs on lower side subpatent, a few longer, numerous shorter, denser along nerves. *Inflorescences* terminal on main stem and branches, furcate, cymes divaricate, scorpioid in flower, 3–10 cm long in fruit, ebracteate; pedicels c. 1 mm long in fruit, curved downwards. *Calyx* 1–1.5 mm long in flower, 1.5 mm long in fruit, divided to base, lobes 0.5–0.8 mm wide, acute. *Corolla* white or dilute bluish, funnel-shaped, 2–3(–4) mm long, c. 3–4 mm in diam., glabrous, lobes ovate-suborbicular, 1(–1.5) mm long; fornicies transverse linear, much wider than long. *Stamens*: filaments and anthers very short, anthers broadly ovate, much smaller than fornicies, not reaching their base. *Pistil*: style very short, stigma indistinct. *Nutlets* ovate in outline, with nearly flat disc, 1.5–2.2 mm long, glochids equally distributed or less dense on disc, bases joined along margin.

Distribution — Widespread in NE, E and southern Africa, Arabia, Afghanistan, Pakistan, Himalayas, India, China, Japan, Taiwan, Indochina, Burma, Thailand; *Malesia*: Sumatra, Borneo, Java, Philippines, Celebes.

Habitat — Not very specialized.

9. *Cynoglossum macrolimbe* Riedl

Cynoglossum macrolimbe Riedl, Linzer Biol. Beitr. 22 (1990) 310. — Type: Brass 22460 (A, LAE), Papua New Guinea, Dayman Mts.

Basal parts and main stem not known, but obviously a much branched stout herb. Branches c. 30 cm long, covered especially in their lower part densely by retrorse or distally by spreading, in dried state brownish hairs. *Leaves* darker green on upper, paler on lower side, with appressed antrorse hairs on the upper, less closely appressed, irregularly directed, along the nerves denser hairs on the lower side, middle leaves lanceolate, rounded-truncate at base, widest below middle, 10–11 by 2.8–3 cm, acute, the upper leaves 4–7 by 1–2 cm. *Cymes* first scorpioid-contracted, later elongate, loose, straight,

composed of about 10 flowers, with horizontally spreading, brownish hairs; pedicels 1.5–3 mm in flower, 12–15 mm long in fruit, more or less bent downwards. *Calyx* 3–3.5 mm long in flower, 6–6.5 mm later on, lobes coherent only at the very base, acute, first 1.5, later 1.8–2 mm wide, covered by antrorse, later on more patent hairs. *Corolla* funnel- to salver-shaped, 4.5–5 mm long, lavender, tube 2 mm long, distinctly shorter than limb, lobes free beyond the middle of the limb, broadly rounded, c. 3.5 mm long and wide, orbicular-obovate to ovate-oblong, spreading; fornicies very short and broad, nearly semilunate, c. 0.8 mm wide. *Stamens*: filaments very short but distinct, attached to middle of tube, anthers slightly incurved at apex, scarcely reaching base of fornicies. *Pistil*: style 2.5–3 mm long, shorter than the nutlets but surpassing them, stigma very small, subcapitate. *Nutlets* slightly immature only known, ovate in outline, 3–3.5 mm long, 2.5 mm wide, with few, very short spines or glochids on the dorsal disc, with several concentric rows of basally widening and partly confluent glochids ventrally and along margin, attached to the short gynobase by the small, apical areola.

Distribution — *Malesia*: New Guinea. Known only from the type collection.

Habitat — No data available.

10. *Cynoglossum novoguineense* Riedl

Cynoglossum novoguineense Riedl, Linzer Biol. Beitr. 22 (1990) 307. — Type: Cruttwell 754 (K), Papua New Guinea, Mt Maneao.

Stout, biennial or perennial plant (base unknown), 50–75 cm at least high. Stem upright, branched in upper part, densely leafy, covered with nearly appressed, antrorse hairs in lower, retrorse hairs in middle and nearly horizontally spreading, white hairs of scarcely 1 mm length in upper part. Basal leaves not seen, stem leaves dark green with short, appressed, soft, antrorse hairs on upper, pale green with irregularly directed, especially along nerves very dense, short, appressed hairs on the lower side, lower stem leaves already dry and vanishing at flowering time, but some still remaining, 6–7.5 by 1.5–2.1 cm, lanceolate, sessile, base rounded or obliquely truncate, widest below middle, acute, middle and upper leaves slightly smaller, 3–6 by up to 1.5 cm wide, even smaller on lateral branches. *Cymes* either crowded at apex or in subdichotomous pairs with a single flower between them, reduced cymes also in axils of upper leaves, sometimes repeatedly branched, scorpioid-contracted at flowering time, later on elongated, straight, leafy in their lower part with smaller leaves than below, with 12–15 flowers in the main cymes; pedicels very short, densely hairy at flowering time, c. 1 mm long, later bent downwards, 6–7 mm long, the lowermost up to 12 mm. *Calyx* 3–3.5 mm long in flower, lobes free to the base or coherent at the very base only, lobes linear-oblong, acute, antrorsely hairy, later accrescent, 6–8 mm long, lobes coherent for the fourth or fifth part, c. 2 mm wide, lanceolate, slightly recurved. *Corolla* intensely blue, salver-shaped or nearly funnel-shaped, 4–5 mm long, 12 mm in diam., tube 2–2.5 mm long, hidden by the calyx, limb spreading, divided at least to the middle into broadly rounded, 4–4.5 mm long and 3–4 mm wide lobes; fornicies trapeziform, slightly shorter

than wide, puberulent. *Stamens*: filaments very short, attached slightly below base of fornices, anthers oblong, scarcely 1 mm long. *Pistil*: style 2–2.5 mm long; stigma very small, capitate. *Nutlets* ovate in outline, subacute, 4.5 mm long, 3.5–4 mm wide, with loosely arranged, slender spines or glochids on dorsal disc, very dense glochids along margin and dense, slender conical glochids or spines ventrally, attached to the gynobase by an areola that covers more than half the length of the ventral surface.

Distribution — *Malesia*: New Guinea, endemic, only known from the type specimen.

Habitat — No data available.

11. *Cynoglossum papuanum* O. Brand

Cynoglossum papuanum Schltr. ex O. Brand, Bot. Jahrb. 62 (1929) 489. — Type: *Keysser* 22 (B, destroyed), Papua New Guinea, Saruwaged Mts.

Erect, sparsely hairy herb. Base and lower *leaves* unknown, upper leaves obovate or oblong, 4–6 by 1.5–2 cm, semiamplexicaulous, acute, covered densely by groups of mineralized cells. *Cymes* terminal, loose, ebracteate or with few bracts near base; lower pedicels longer than calyx and bent downwards in fruit. *Sepals* ovate, acute, sparsely appressed hairy, 5 mm long, after flowering elongated to 6–7 mm. *Corolla* shortly and broadly cylindrical, twice as long as calyx; fornices large, trapeziform. *Stamens* inserted at the middle of the tube. *Gynobasis* depressed pyramidalate, with 4 large excavations, about as long as style. *Nutlets* 6 mm in diam., marginate, densely spiny, spines denser in the margin and ventrally than on the dorsal surface; embryo 4 mm long with nearly orbicular cotyledons and very short rootlet.

Distribution — *Malesia*: New Guinea, only known from the type collection.

Note — As the type has been destroyed and no new material is available, the above description is a translation of the original diagnosis, in which several important characters have not been mentioned while other, unusual characters are described in detail.

12. *Cynoglossum timorense* Riedl

Cynoglossum timorense Riedl, Blumea 38 (1994) 463. — Type: *van Steenis* 18303 (L holo), Timor, Mt Perdido.

Annual (?), 30–40 cm high. Stem branched from near the base, covered by patent or retrorse hairs in the lower, antrorse hairs in the upper part. *Leaves* lanceolate to obovate or oblong, tapering towards petiole, acute to shortly acuminate, nervature distinct, reticulate on lower side, covered by nearly spreading, stiff, bristly hairs, petiole of lower leaves 5–10 mm long, blade 1.5 by 0.7 cm, petiole of middle leaves shorter, blade 3–3.5 by 0.9–1 cm, petiole of upper leaves 0–2 mm long, blade 1.5–2.5 by 0.6 cm. *Inflorescence* loose, elongated up to 15 cm after flowering, with leafy bracts in the lower, ebracteate in the upper part; pedicels filiform, 1 mm long in flower, elongated to 3–7 (–15) mm in fruit, curved downwards. *Calyx* 1.5–2 mm in flower, 2–2.5 mm in fruit, antrorsely strigillose, lobes free to the base, 0.8–1 mm wide, subacute or acute. *Corolla*

campanulate to funnel-shaped, 2.5(–3) mm long, 4.5 mm in diam., glabrous, tube shorter than calyx, lobes elliptical, 1.5 mm long; fornice trapeziform to subquadrate, indistinctly emarginate, subinvolute at apex. *Stamens*: anthers subsessile a little below the fornice, ovoid, 0.6 mm long. *Pistil*: style 0.3 mm long in flower, hidden by the nutlets, without distinct stigma. *Nutlets* ovate in outline, 2–2.5 mm long, 1.5 mm wide, with a flat dorsal disc, densely glochidiate in margin with confluent bases of glochids, glochids evenly distributed on disc.

Distribution — *Malesia*: Lesser Sunda Islands (Lombok, Flores, Timor).

Habitat — On naked limestone peak (type), roadsides at 1750–2100 m altitude.

Notes — 1. A specimen from Sumbawa is characterized by larger leaves that are serrate by the thickened bases of marginal bristles and distinctly larger calyx with sharply acute lobes, that are spreading star-like. It is not clear whether this is within the normal amplitude of variation or whether this plant represents a separate taxon probably on the infraspecific level.

2. Several plants from Java are similar to *C. timorens* in their small nutlets, comparatively long, slender fruiting pedicels and small leaves. It is not quite clear whether they should be assigned to *C. javanicum*, that seems to be extremely variable, or to *C. timorens*.

13. *Cynoglossum spec. A*

Perennial herbs, stems arising from rooting, subhorizontal, subterranean shoots, 40–50 cm high, with few branches, with long, spreading to retrorse, fairly dense, flexuous hairs. *Leaves* ovate-lanceolate to lanceolate, petiole 0.5–1 cm in lower, 0–0.3 cm in upper leaves, blade 7–8 by 2–2.5 cm in lower, 2.5–5 by 0.6–1.2 cm in upper leaves, 2–6.5 by 0.6–1.2 cm in sterile, lateral branchlets, tapering towards base or rounded, sessile, acute, with 5–7 pairs of primary lateral nerves especially distinct on lower side, hairs subpatent, irregularly directed on upper, rigid, arising from mineralized cells on lower side. *Cymes* in main stem paired, in lateral branches single, ebracteate, short, very loose, lowermost flower below uppermost leaves, extra-axillary; pedicel of lowermost flower 2–2.5 cm long, others 0.4–1.2 cm after flowering, very short in flower, with very long, curved, spreading hairs. *Calyx* c. 2.5 mm long in flower, scarcely accrescent, divided to base, lobes ovate, 1–1.2 mm wide, acute, with dense, long, spreading to antrorse hairs crowded in centre of lobes. *Corolla* short campanulate to funnel-shaped, colour not known, 3.5 mm long, 5–5.5 mm in diam., glabrous or with few spreading hairs on lobes, tube included in calyx, lobes oblong, c. 1.5 mm long, 1.2 mm wide; fornice transversely linear, 0.5–0.6 mm wide, 0.15 mm long. *Stamens*: anthers nearly sessile, placed below fornice. *Pistil*: style not surpassing ovary in juvenile state. *Nutlets* (immature only known) ovate-suborbicular in outline, c. 2 mm long, glochids dense ventrally and along margin, few on flat disc.

Distribution — Known only from a single collection from Lombok, *Elbert 1366*, 27 May 1909 (seen from L).

Habitat — Bushy grassland, 3200–3500 m altitude, on loose, volcanic gravel.

EHRETIA

Ehretia L., Syst., ed. 10 (1759) 936; I.M. Johnston, J. Arnold Arbor. 32 (1951) 19. — Type species: *Ehretia tinifolia* L.

Trees or shrubs. *Leaves* small to large, alternate, margin entire or serrate, sometimes wavy. *Inflorescences* terminal and/or lateral, branched or unbranched, sometimes arranged in corymb- or panicle-like structures. *Calyx*-lobes 5, separate from the beginning. *Corolla* white or pale yellow, with elongate-cylindrical or campanulate tube and spreading to recurved lobes. *Stamens*: anthers exserted as a rule, on filiform filaments. *Ovary*: style terminal, with two branches free in the uppermost part or to the middle; stigmas 2, capitate or elongate. *Fruit* a subglobose drupe, yellow, orange or reddish, with two separate pyrenes sometimes divided again into 4 one-seeded parts. *Pollen* spheroidal to prolate-spheroidal or subprolate, finely reticulate or striate-reticulate, 3-colpate or 3-colporoidate. — **Fig. 6.**

Distribution — About 50 species in the tropics and subtropics of Africa, Asia and Australia, 3 species in America. In *Malesia* 12 species.

Uses — Medicinal use is mentioned for *E. philippinensis* and *E. resinosa* in Jansen et al. (eds.), Plant Resources of SE Asia (PROSEA Handb.), Basic List (1991) 230.

Notes — 1. Crystal druses present in vascular parenchyma.

2. Chromosome numbers given as $2n = 26, 32, 40$.

3. The genera *Ehretia* and *Bourreria* are very close to each other. The latter generally has been regarded as exclusively American, but Thulin (1987) found that also some African species belong to it. The main distinguishing character is the calyx of the young bud which is undivided in *Bourreria* splitting into 2 to 5 lobes when opening, while 5 separate lobes are present from the beginning in true *Ehretia*. The pyrenes are always separating into two one-seeded units in *Bourreria*, while in *Ehretia* there are two sections, *Ehretia* s.str. with 2 two-seeded pyrenes not further dividing at maturity, and *Bourreroides* Benth. & Hook. f. with 4 separate units in the end. •

Reference: Thulin, M., Nordic J. Bot. 7 (1987) 413.

KEY TO THE SPECIES

- 1a. Leaves serrate to irregularly dentate. Inflorescence paniculoid or thyrsoid **1. *E. acuminata***
- b. Leaves entire or with few irregular teeth. Inflorescence corymbose or with few cymose branches **2**
- 2a. Cymes few-flowered, always axillary, bracteate; lower bracts up to 10 mm long .. **8. *E. papuana***
- b. Inflorescence terminal or axillary, with branched or unbranched cymes or corymbose, without or with few bracts at base of branches **3**
- 3a. Tube of corolla 3.5–5 times as long as the calyx; lobes one third, rarely up to half as long as tube, recurved. Fruit up to 10 mm long **4. *E. javanica***

- b. Tube of the corolla shorter compared to the calyx and lobes. Fruit 8 mm long or shorter 4
- 4a. Anthers sagittate, with a narrow but distinct sinus between their lower ends. Often also veins of higher order distinct, forming a dense network ... **11. E. resinosa**
- b. Anthers not sagittate, linear, sometimes widened and rounded at base. Only primary nerves prominent 5
- 5a. Inflorescence branched, with 1–5 flowers all on one side of each branch, on short pedicels (0.5–1 mm) 6
- b. Inflorescence branched, flowers single (rarely 2 or 3) terminal on branches of ultimate order, not all on one side of main branches 8
- 6a. Inflorescence glabrous **3. E. dichotoma**
- b. Inflorescence shortly pubescent, sometimes with glands 7
- 7a. Leaves ovate to lanceolate, with distant primary nerves usually 1 cm or more apart at their base **6. E. laevis**
- b. Leaves obovate to oblanceolate, sometimes emarginate at apex, with very dense primary nerves less than 1 cm apart at their base **9. E. parallela**
- 8a. Inflorescence glabrous or nearly glabrous 9
- b. Inflorescence hairy 10
- 9a. Leaves acute or acuminate. Calyx 1.2–1.5 mm long, cleft to middle or a little beyond, lobes glabrous or with few hairs along margin. Style cleft for about 0.8 mm **10. E. philippinensis**
- b. Leaves rarely acute, usually obtuse or emarginate. Calyx 2.5 mm long, cleft for about 2 mm, lobes densely ciliate along margin. Style cleft for most of its length **12. E. timorensis**
- 10a. Scandent shrubs. Calyx densely covered with very short reddish, strigillose hairs. Young branches with loose patent bristles sometimes thorn-like with broader base **2. E. asperula**
- b. Trees. Calyx without reddish hairs, sometimes ciliate along margin and/or covered with white pustules. Young branches glabrous 11
- 11a. Corolla-tube distinctly longer than calyx. Calyx lobes with patent, long hairs along margin, glabrous on surface **7. E. moluccana**
- b. Corolla-tube included in calyx. Calyx lobes ciliate along margin, white pustulate on surface **5. E. keyensis**

1. *Ehretia acuminata* R. Br.

Ehretia acuminata R. Br., Prodr. Fl. Nov. Holl. (1810) 497; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 690; I.M. Johnston, J. Arnold Arbor. 32 (1951) 21; Backer & Bakh. f., Fl. Java 2 (1965) 459. — Type: *R. Brown s.n.* (K holotype), Australia, Port Jackson.

Ehretia serrata Roxb., Hort. Beng. (1814) 17, nomen; Fl. Ind., ed. Carey & Wall., 2 (1824) 340, descr.; Miq., Fl. Ind. Bat. 2 (1856) 920; Koord., Exk. Fl. Java 3 (1912) 127. — Type: Cultivated in Calcutta Bot. Garden.

Ehretia ovalifolia Hassk., Cat. Hort. Bogor. (1844) 137. — Type: Cultivated in Bogor (Buitenzorg) Bot. Garden, ex Japan.

Ehretia polyantha DC., Prodr. 9 (1845) 503; Miq., Fl. Ind. Bat. 2 (1856) 920. — *Ehretia acuminata* R. Br. var. *polyantha* (DC.) I.M. Johnston, J. Arnold Arbor. 32 (1951) 24. — Type: Perrotet (GE), Philippines.

Ehretia acuminata R. Br. var. *pyrifolia* (D. Don) I.M. Johnston, J. Arnold Arbor. 32 (1951) 23. — Type: Wallich (K), Nepal.

Tree up to 25 m high. Young branches (blackish) brown, glabrous, older branches grey. *Leaves* lanceolate to ovate-lanceolate or oblong, (3–)5–15(–18) by (1.5–)2–8 cm, finely serrate, serrate, crenate-dentate to grossly dentate, indistinctly petiolate, base obliquely truncate to rounded, apex acute, with 4–7 nerves on each side, upper side glabrous, lower side with hairs along main nerves. *Inflorescence* terminal on main and lateral branches, paniculoid, with numerous flowers; pedicels 1–2.5 mm long. *Calyx* cup-shaped, 1.5 mm long, 2 mm wide in flower, lobes 5, free beyond middle, laterally overlapping in flower, with hairs along margin. *Corolla* funnel-shaped, 2–2.5 mm long, 4–5 mm in diam., lobes oblong, obtuse, 1.5(–2) mm long. *Stamens* exserted. *Pistil*: style divided for 1/3, branches widening towards indistinct stigmata. *Fruit* globose, c. 7 mm in diam.

Distribution — Australia, China; *Malesia*: Java, Philippines, Lesser Sunda Islands (Bali, Sumbawa, Flores, Timor), Moluccas, New Guinea.

Habitat — In forests.

Note — The species is highly variable, but variation does not follow any geographical pattern as supposed by Johnston (1951). The assumption that Malesian specimens can be separated in a var. *pyrifolia* does not hold.

2. *Ehretia asperula* Zoll. & Mor.

Ehretia asperula Zoll. & Mor. in Mor., Syst. Verz. Zoll. (1845–46) 52; I.M. Johnston, J. Arnold Arbor. 32 (1951) 106; Backer & Bakh. f., Fl. Java 2 (1965) 460, in adnot. — Type: Zollinger 1548, Java.

Climbing shrub. Young branches reddish to greyish brown, covered with loose patent bristles that often have a bulbous base. *Leaves*: petiole (0.5–)0.8–1(–1.5) cm; blade lanceolate to oblong-lanceolate, (1.5–)3–15 by 0.8–5.5 cm, entire or widely repand-dentate, base narrowly rounded to obliquely truncate, apex acuminate, nerves (4–)5(–6) on each side, glabrous on both sides or with few hairs along nerves beneath. *Inflorescence* terminal and lateral on short branches, loosely corymbose to paniculoid, patent bristly, with numerous flowers; pedicels 0.8–3 mm long. *Calyx* cup-shaped, 1.2–1.5 mm long, 2.5–3 mm wide, lobes free for 1/3 to 1/2, triangular, densely strigillose with very short, reddish hairs. *Corolla* broadly and shortly campanulate, white, 1.5–1.8 mm long, 3.5–4 mm in diam., lobes wider than long, 1 mm long, c. 2 mm wide, broadly rounded. *Stamens* very long exserted. *Pistil*: style 3.5 mm long, the branches free for 1/3 or a little more, the stigmata indistinct. *Fruit* globose to subglobose, c. 3.5 mm in diameter.

Distribution — Hainan, Vietnam; *Malesia*: Sumatra, Peninsular Malaysia (Johore), Borneo, Java.

Habitat — Primary forest, upper dipterocarpous forest.



Fig. 6. *Ehretia dichotoma* Blume. a. Top of flowering twig; b. flower (Blume 692). Drawing by M. Spitteler.

3. *Ehretia dichotoma* Blume

- Ehretia dichotoma* Blume, Bijdr. (1826) 842; I. M. Johnston, J. Arnold Arbor. 32 (1951) 109; Backer & Bakh. f., Fl. Java 2 (1965) 460. — Type: *Blume s. n.* (L holo), Java, Mt Burangrang.
Ehretia laurifolia Decne., Nouv. Ann. Mus. Paris 3 (1834) 395. — Type: *Herb. Timor*. 67.
 ? *Ehretia lucida* Span., Linnaea 15 (1841) 334. — Type: not indicated.
Ehretia timorensis auct. non Decne.: Ng in Tree Fl. Malaya 4 (1989) 62; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1966) 101, f. 3 (see note).

Tree, rarely more than 15 m high. Branches brownish to greyish, youngest parts sometimes dark brown, glabrous. *Leaves*: petiole 6–15 mm; blade lanceolate, rarely ovate-lanceolate, 2.5–12 by 1–6 cm, entire, wavy or very rarely repanded-dentate, obliquely rounded to truncate at base, apex acute to acuminate, nerves 5–7 on each side, at wide angles to midrib, the same colour on both sides or paler beneath, glabrous on upper, with hairs in axils of primary nerves at lower side, sometimes folded along midrib. *Inflorescence* terminal on young, lateral branches or axillary, subcorymbose, flowers all at one side of branches of last order, sparsely hairy, with few to numerous flowers; pedi-

cels less than 1 mm. *Calyx* campanulate, 2(–2.5) mm long, 2.25 mm wide, lobes free for 1/3, hairs along margins. *Corolla* white, 4–4.5 mm long, upper border of tube 3.5 mm wide, tube subcylindrical-obconical, lobes reflexed, 2.5 mm long, with revolute margins. *Stamens* very long exserted. *Pistil*: style 5–5.5 mm long, free branches 1–1.25 mm, stigmata 2, discoid-subcapitate, distinct also by colour. *Fruit* globose, 3.5–4(–5) mm in diam. — **Fig. 6.**

Distribution — Andaman Islands, Vietnam; *Malesia*: Sumatra, Malay Peninsula, Borneo, Java, Celebes, Lesser Sunda Islands (Flores, Timor).

Habitat — Dry, evergreen forests, plains, below 1000 m altitude.

Note — In literature on the Malay Peninsula and also in the Tree Flora Sabah & Sarawak, the species has been called *E. timorensis* or *E. laevis* var. *timorensis*, from which it is widely different.

4. *Ehretia javanica* Blume

Ehretia javanica Blume, Bijdr. (1826) 842; Backer & Bakh. f., Fl. Java 2 (1965) 460. — Type: *Blume s. n.* (L holo), Java.

Tree up to 30 m high. Youngest branches dark reddish brown, older ones greyish brown, glabrous. *Leaves*: petioles 1–3.5 cm long; blade broadly lanceolate, ovate-lanceolate, oblong-lanceolate, obovate or suborbicular, 2–13 by 1–7.5 cm, margin entire or somewhat wavy, base obliquely truncate to rounded, apex acute, acuminate or obtuse, nerves 4–6(–7) on each side of midrib, upper side glabrous or with a very few hairs, lower side glabrous. *Inflorescence* terminal on short, lateral branches, subcorymbose, branchlets of last order at very acute angles, glabrous or with very few hairs; pedicels 1–3 cm long. *Calyx* obconical to cup-shaped, sepals 2–3, mostly 2.5 mm long and wide, loosely strigillose, lobes free for 2/3, narrowly triangular with revolute margins. *Corolla* funnel-shaped, 9–10 mm long, 7–8 mm in diam., tube cylindrical-campanulate, lobes explanate, 3 mm long, rounded at apex. *Stamens* shortly exserted(?). *Pistil*: style 12–13 mm long, branches suberect, 2 mm long, stigmata indistinct. *Fruit* ellipsoidal, 10 mm long, 7–8 mm in diam. when compressed.

Distribution — *Malesia*: Java, (Borneo?), Lesser Sunda Islands (Bali, Sumbawa, Flores).

Habitat — Forest, mountain slopes, between 500 and 1200 m altitude.

5. *Ehretia keyensis* Warb.

Ehretia keyensis Warb., Bot. Jahrb. 13 (1891) 424. — Type: from Key Islands (B holo, destroyed).

Tree, 5–10 m high. Branches dilute greyish brown to dark brown and patchy pale grey to fawn, glabrous. *Leaves*: petiole 0.5–2 cm; blade lanceolate to ovate-lanceolate, 2.5–13 by 0.8–7 cm, margin entire, base obliquely truncate to broadly rounded, apex acute to acuminate, nerves 4–7 on each side, glabrous on both sides. *Inflorescence* subterminal to axillary, loosely corymbose with numerous branches, branches with long, stiff, patent hairs, flowers very numerous; pedicels 0.5–5 mm long. *Calyx* cup-shaped,

later flattish salver-shaped, 1.2 mm long, 1.5 mm wide in flower, up to 4 mm in fruit, white pustulate on surface, ciliate along margin of lobes, lobes free beyond middle, triangular to oblong lanceolate. *Corolla* white, as long as calyx, tube slightly shorter than calyx, campanulate, limb 3.5 mm in diam., lobes explanate to slightly recurved, rounded, 1.3 by 1.1 mm. *Stamens* exserted. *Pistil*: style c. 1.5 mm long, divided for 2/3; stigmata subcapitate. *Fruit* globose, 2–2.5 mm in diam.

Distribution — *Malesia*: Key Islands, New Guinea.

Habitat — Swamp fringes, forest remnants, regrowth, thicket and scrubland.

6. *Ehretia laevis* Roxb.

Ehretia laevis Roxb., Pl. Corom. 1 (1796) 42, t. 56; I.M. Johnston, J. Arnold Arbor. 32 (1951) 107.

— Type: Plate in Roxburgh, l.c. 'Serigade of the Telingas'.

Shrub or tree. Branches greyish, the youngest ones dark reddish brown, glabrous. *Leaves*: petiole c. 1–2.5 cm long; blade oblong to suborbicular or oblong-lanceolate, 3–9 (–18) by 3–5 (–11) cm, margin entire, base broadly rounded to truncate, apex acuminate, rounded or emarginate, nerves 4 or 5 on each side, upper side glabrous, lower side with hairs in the axils of lowest primary nerves. *Inflorescence* axillary, corymbose, with very short hairs, flowers few to many. *Flowers* subsessile or pedicels up to 1 mm long. *Calyx* cup-shaped, (1.2–)1.5–1.8 mm long, c. 3 mm wide, glabrescent, lobes lanceolate, obtuse, free for 2/3. *Corolla* white, 2–2.3 mm long, up to 5 mm in diam., tube cylindrical, surpassing calyx for c. 0.5 mm, lobes explanate to recurved, c. 2 mm long, longer than wide, rounded with often revolute margins. *Stamens* exserted. *Pistil*: style 2.5 mm long, divaricately forked to at least middle, stigmata indistinct. *Fruit* globose, 3–4 mm in diam.

Distribution — India, Hainan, Vietnam, Burma; *Malesia*: Malay Peninsula.

Habitat — No data available.

7. *Ehretia moluccana* Riedl

Ehretia moluccana Riedl, Blumea 38 (1994) 463. — Type: *Beguín* 1695 (L. holo), Ternate.

Tree (?). Young branches first dark brown, later greyish, glabrous. *Leaves*: petiole 0.5–3 cm; blade lanceolate to oblong-lanceolate or ovate-lanceolate, (3–)5–18 by 1.5–9 cm, margin entire to wavy, base truncate, apex acute to acuminate, nerves 5–7 on each side, glabrous on both sides. *Inflorescence* axillary or terminal on short branches, corymbose with long primary branches, at length broadly expanded, flowers numerous in subcapitate groups crowded at end of branches, with loose, white, patent hairs; pedicels less than 1 mm long. *Calyx* broadly cup-shaped, 1.5 mm long, 2 mm in diam., with loose, patent hairs along margin of lobes, lobes free for 3/4, lanceolate. *Corolla* white, 3.5 mm long, c. 5 mm in diam., tube cylindrical-campanulate, gradually widening towards apex, lobes reflexed to subexplanate, 2.5 mm long, 1 mm wide at base, rounded, but seemingly acute by revolute margins. *Stamens*: filaments long exserted, anthers linear, 1 mm long. *Pistil*: style 4–4.5 mm long, forked for 0.8–1 mm, branches more or less erect; stigmata small, subcapitate, fairly indistinct. *Fruit* not seen.

Distribution — *Malesia*: Moluccas (Ceram, Ternate, Halmahera).

Habitat — Primary forest at very low altitude.

Vernacular name — Gomadedeo.

Uses — Local use as a disinfectant after child-birth and as a contraceptive.

8. *Ehretia papuana* S. Moore

Ehretia papuana S. Moore, J. Bot. 61 (1923) Suppl., 36. — Type: *Forbes s.n.* (BM holo), New Guinea, Kerepunu.

Shrub (?). Branches fistulose, somewhat compressed, glabrous. *Leaves*: petiole slender, 3–6 cm long; blade broadly ovate-rounded, 6–8 by 5–7 cm, margin entire or somewhat repand-dentate, base broadly truncate, apex obtuse, nerves 4 or 5 on each side, between main nerves densely reticulate on lower side, glabrous on both sides. *Inflorescence* axillary, shorter than the subtending leaves, few-flowered; bracts leafy, lanceolate, 0.2–1 cm long; pedicels c. 2.5 mm long. *Calyx* 5.5 mm long, lobes free to nearly the middle, ovate, more or less obtuse. *Corolla* short-campanulate, tube slightly shorter than calyx, lobes oblong-spathulate, 3 mm long. *Stamens* shortly exserted, anthers oblong, 1.25 mm long. *Pistil*: style 2.5 mm long, forked divaricately for about 0.25 mm. Mature *nutlets* not seen.

Distribution — *Malesia*: New Guinea.

Habitat — No data available.

Note — The species seems to be known only from the type collection (not seen), but is very distinct from all others as far as can be judged from the author's description, that is translated here.

9. *Ehretia parallela* C.B. Clarke

Ehretia parallela C.B. Clarke in Hook. f., Fl. Brit. India 4 (1885) 143; Ridl., Fl. Malay Penins. 2 (1923) 442; Ng in Tree Fl. Malaya 4 (1989) 63. — Type: *Griffith K.D. 6004* (K holo; W), Burma, Irrawaddy.

Tree. Branches glabrous, greyish. *Leaves*: petiole 0.3–0.5 mm; blade obovate, 1.2–4 by 0.5–2.2 cm, margin entire, base obliquely truncate, apex broadly rounded to obtuse, nerves parallel, 6–9 on each side, glabrous on both sides. *Inflorescence* axillary on a short peduncle (1–2.5 cm), with patent hairs; flowers all on one side of branches of last order, subsessile or on pedicels of 0.5 mm. *Calyx* 2 mm long, shortly strigillose, lobes free for at least 2/3, triangular. *Corolla* white, 7–10 mm long. *Fruit* depressed globose, 2.5 mm long, 3 mm in diam.

Distribution — Burma; *Malesia*: Malay Peninsula.

Habitat — No data available.

10. *Ehretia philippinensis* A.DC.

Ehretia philippinensis A.DC. in DC., Prodr. 9 (1845) 504; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 691. — Type: *Cuming 471* (G holo), Philippines.

Small tree 4–5 m high. Young branches brown to greenish brown, glabrous. *Leaves*: petiole 1–3 cm long; blade broadly lanceolate to oblong-lanceolate or ovate-lanceolate, (3–)4–15 by 1.5–7.5(–8) cm, margin entire, base attenuate, obliquely truncate, apex acute or acuminate, nerves 4–6 on each side, glabrous or subglabrous on both sides. *Inflorescence* on short, lateral branches or axillary, corymbose, with numerous flowers. *Calyx* broadly cup-shaped, 1.25–1.5 mm long, 1.25–2 mm wide, glabrous or with few hairs along margin of lobes, lobes free to the middle or beyond, triangular. *Corolla* white, 3.5–4(–5) mm long, c. 5 mm in diam., tube cylindrical-campanulate, lobes more or less reflexed, broadly rounded, c. 2.5 mm long. *Stamens* long exserted. *Pistil*: style 4.5–6 mm long, forked for 0.8 mm; stigmata capitate, distinct. *Fruit* subglobose, 3–4 mm in diam.

Distribution — *Malesia*: Philippines (Luzon, Mindanao, Palawan).

Habitat — In forests along rivers and secondary growth at low and medium altitudes.

Note — In the type collection the flowers are especially small.

11. *Ehretia resinosa* Hance

Ehretia resinosa Hance, J. Bot. 18 (1880) 299; I. M. Johnston, J. Arnold Arbor. 32 (1951) 103. — Type: Swinhoe 12333, Taiwan.

Ehretia navesii Vidal, Rev. Pl. Vasc. Filip. (1886) 194. — Types: Vidal 471, 473.

Tree. Branches dark brown first, greyish to brownish at a later stage, glabrous. *Leaves*: petiole 0.8–3 cm long; blade broadly ovate to ovate-lanceolate, 2–20 by 1.2–10 cm, margin entire, base broadly rounded to subcordate, apex subacute, acute to acuminate, 5–7 primary nerves on each side, with a dense network of minor nerves between them, glabrous to subglabrous on upper side, subglabrous or sparsely hairy mainly along nerves on lower side, young leaves with very dense hairs on lower side. *Inflorescences* on short, lateral branches, densely corymbose, with dense, patent hairs, flowers numerous; pedicels 1–4 mm long. *Calyx* campanulate, 3–4 mm long, c. 2 mm wide in flower, later on lobes patent, 5 mm in diam., densely covered by patent hairs, lobes linear-oblong, obtuse, free to near base. *Corolla* white, 5–6 mm long, up to 9 mm in diam., tube cylindrical-campanulate, lobes 4.5–5 mm long, rounded, reflexed to sub-explanate. *Stamens* long exserted, anthers sagittate. *Pistil*: styles 7 mm long, widened towards apex, forked for 1.5 mm, stigmata fairly indistinct. *Fruit* subglobose, 4–5 mm in diam.

Distribution — Taiwan; *Malesia*: Philippines (Luzon).

Habitat — No data available.

Note — A comparison of plants from Taiwan and from Luzon shows practically no differences, as already Johnston (1951) has suggested.

12. *Ehretia timorensis* Decne.

Ehretia timorensis Decne., Nouv. Ann. Mus. Paris. 3 (1834) 395, non Ridley, Fl. Malay Penins. 2 (1923) 442, nec Ng in Tree Fl. Malaya 4 (1989) 63. — Type: *Anonymous* (P holo), Timor.

Tree (?). Youngest branches dark reddish brown or blackish brown when dry, older ones brownish to greyish brown, often fissured, glabrous. *Leaves*: petiole 0.8–2.2 cm long; blade broadly ovate-lanceolate to obovate, 3–7 by 1.5–4.5 cm, base obliquely truncate, apex obtuse or emarginate, often cuspidate, sometimes folded along midrib, nerves distinct only on lower side, (5–)6–7 on each side, glabrous or with a very few hairs on upper, tomentose in the axils of the primary nerves on the lower side. *Inflorescence* subapical or on lateral branches, corymbose-paniculoid, glabrous, often with flexuous branches, loose, many-flowered; pedicels 0.5–5 mm (in fruit). Fruiting *calyx* up to 2.5 mm long, 4.5 mm in diam., lobes 2 mm long, triangular, ciliate along margins. *Fruit* globose or a little depressed, 4–5 mm in diam., keeled at margin of carpels, with the remnants of the style that is breaking at point of branching.

Distribution — *Malesia*: Lesser Sunda Islands (Timor).

Note — The species is only known from the type collection from which the description was prepared. Flowers are unknown. There are marked differences with all other species in the Malesian area.

DOUBTFUL SPECIES, PROBABLY TO BE EXCLUDED

Ehretia uniflora Roxb., Hort. Beng. (1814) 84, nomen; Fl. Ind., ed. Carey & Wall., 2 (1824) 344. — Type not indicated.

“Shrubby, twiggy. Leaves crowded, subsessile, oblong, entire, hairy. Flowers solitary, sub-sessile. Drupe with 4 one-celled nuts.”

Distribution — *Malesia*: Moluccas.

Note — Probably not an *Ehretia*.

HELIOTROPIUM

Heliotropium L., Sp. Pl. (1753) 130; Gen. Pl., ed. 5 (1754) 164. — Type species: *Heliotropium europaeum* L.

Annual or perennial herbs or subshrubs. *Leaves* large to small, alternate, petiolate or sessile. *Inflorescence* usually a unilateral, scorpioid cyme, sometimes 2 cymes close together on dichotomous branches or even a greater number of short cymes crowded together in a head-like manner, with or without bracts that may be foliose or very small and sometimes confined to lower part of cyme. *Corolla* tubular, funnel-shaped or hypocrateriform, white, yellowish to yellow, purple or purplish violet, tube often with an inflated part where the anthers are inserted. *Stamens* included with very short filaments. *Pistil*: style apical, sometimes strongly reduced to nearly absent below stigma, free from the ovary as soon as the pyrenes are separating; stigma¹ a ring-like structure round the style. Mature *nutlets* either remaining undivided with 4 locules or by reduction finally

1) For the sake of convenience the whole structure from the stigmatic ring upwards is as a rule called stigma; it may be cylindric with a basal disc, conical, or cushion-shaped.

with only one fertile locule, or separating into two bilocular pyrenes, most often these pyrenes again separating into 2 unilocular nutlets; surface of nutlets smooth or sculptured in various ways. — **Fig. 7, 8.**

Distribution — A genus of about 250 species in the warm and warm temperate zones of all continents.

Habitat — *Heliotropium* species occur in very diverse habitats, though in general drier places are preferred. Some species are weeds, often introduced from the New World at an early date and now widespread in the palaeotropics.

Uses — *Heliotropium indicum* is reported to be used as a medicinal plant and also sometimes for the production of beverages and dyes [Jansen et al. (eds.), Plant Resources of SE Asia (PROSEA Handb.), Basic List (1991) 234]. *Heliotropium arborescens*, better known under its synonym *H. peruvianum*, is widely cultivated as an ornamental plant and may have escaped cultivation in some places, as it is mentioned for the Malaysian region, though cultivation seems to have become obsolete.

Chromosomes — At least four basic chromosome numbers are known in the genus that are not closely related to the taxonomic position of the species from the scattered data available. There are polyploid series known from the basic numbers $x = 7$ and 8, while from the basic numbers $x = 9, 11$ and 13 only diploids were found so far.

Notes — 1. *Cochranea* Miers is sometimes regarded as a separate genus mainly South American in distribution, but extending to the Malesian region with *Heliotropium anchusaefolium*. The differences, however, do not seem to justify separation, as they are by no means more profound than those existing between subgenera and sections normally included in *Heliotropium*; *H. anchusaefolium* is the type species of section *Helio-phytum*, moreover, and does not even belong to *Cochranea*.

2. Infrageneric classification suffers from the absence of a recent treatment including both Old World and New World species since the time of De Candolle's Prodrômus. There is a lack of correspondence between the various local treatments. Malesian native and introduced species belong to sections *Helio-phytum*, *Tiaridium*, *Halmyrophila* (= *Platygyne*), *Heliothamnus* and *Orthostachys* according to the most recent system of Johnston [Contr. Gray Herb. 81 (1928) 4], which, however, covers South American taxa only.

KEY TO THE SPECIES

- 1a. Stigma an umbrella-shaped disc on a short style. Plant more or less succulent **4. *H. curassavicum***
- b. Stigma conical or a ring-like structure surpassed by a tubular apical part. Plants not succulent 2
- 2a. Leaves broad, ovate to oblong 3
- b. Leaves narrowly linear to lanceolate. Fruit not ribbed, separating into 4 nutlets 6
- 3a. Fruit separating into 2 bilocular pyrenes. Corolla villous inside **1. *H. amplexicaule***

- b. Fruit not dividing at all or separating into 4 unilocular nutlets. Corolla not villous inside. 4
- 4a. Inflorescence corymbose, composed of branched cymes. Fruit separating into 4 nutlets **2. *H. arborescens***
- b. Inflorescence spike-like, elongate, not corymbose. Fruit remaining undivided 5
- 5a. Apex of carpels profoundly bidentate; carpels 2.5–3 mm long, strongly divergent at last **6. *H. indicum***
- b. Apex of carpels entire or slightly bidentate; carpels 4–5 mm long, not or scarcely divergent at last **5. *H. elongatum***
- 6a. Inflorescence without bracts. Leaves elliptic to obovate, with silky hairs **8. *H. ovalifolium***
- b. Inflorescence with bracts, or flowers in axils of leaves 7
- 7a. Stems and branches more or less prostrate 8
- b. Stems and branches erect or branches more or less divaricate 9
- 8a. Flowers single in axils of leaves, crowded apically **10. *H. scabrum***
- b. Flowers in terminal short, straight cymes, bracts and flowers alternating on each side **3. *H. brevifolium***
- 9a. Flowers in very dense cymes without any free space between them. Bracts sharply acute, needle-like. Tube of corolla long and slender, strongly inflated by the stamens, surpassing the calyx in length **11. *H. ventricosum***
- b. Flowers not so dense, arranged in 3–8 mm distance of each other. Bracts not so sharply acute, not needle-like. Tube of corolla shorter, usually not or scarcely surpassing the calyx, only weakly inflated by stamens 10
- 10a. Style about 1.5 to 2.5 times as long as stigma. Calyx c. 2.5 mm long **9. *H. paniculatum***
- b. Style about as long as stigma. Calyx c. 1.5 mm long **7. *H. madurense***

1. *Heliotropium amplexicaule* Vahl

Heliotropium amplexicaule Vahl, Symb. Bot. 3 (1794) 21; I.M. Johnston, Contr. Gray Herb. 81 (1928) 21. — Type: *Thouin*, Brazil.

Heliotropium anchusaefolium Poir., Encycl. Suppl. 3 (1813) 23. — *Cochranea anchusifolia* (Poir.) Guerke in Engl. & Prantl, Nat. Pflanzenfam. 4, 3a (1894) 97; Backer & Bakh. f., Fl. Java 2 (1965) 462.

Perennial herb, 30–50 cm high. Stem ascending, much branched. *Leaves* more or less crowded, sessile, 4–7 cm long, 1–2 mm wide, oblong, tapering towards base, apex acute, nerves impressed above, prominent beneath, covered with patent bristles on both sides. *Cymes* terminal, branched, 10–15 cm long, with short glandular and longer normal hairs, without bracts. *Calyx* 4 mm long in flower, slightly accrescent, with 5 linear lobes free to near the base, hairs like inflorescence. *Corolla* hairy outside, tube yellow, slightly longer than calyx, hairy above anthers inside, limb explanate, dark purple from a pale base, 6–8 mm in diam., with 5 shallow lobes, plicate. *Stamens* 5, anthers nearly sessile, oblong. *Pistil*: style shorter than the stigma; stigma conical from an annulate

base. *Fruit* breaking up into 2 two-loculate carpels, with membranous pericarp, glabrous, with 2 longitudinal grooves, 3 mm high.

Distribution — South America. Now widespread in tropical regions; *Malesia*: Java, formerly cultivated, now as an escape near Bogor (according to Backer & Bakhuizen f., l.c.).

Habitat — No data available.

2. *Heliotropium arborescens* L.

Heliotropium arborescens L., Syst. Nat., ed. 10 (1759) 913. — *Heliotropium peruvianum* L., Sp. Pl., ed. 2 (1762) 187, nom. superfl.; Backer & Bakh. f., Fl. Java 2 (1965) 461. — Type: Plate in Mill., Gard. Dict. (1757) 96, pl. 144.

Perennial herb, sometimes with woody base, in its original home also shrub up to 2 m high. Stem much branched. *Leaves* ovate to oblong-elliptic; petiole short, rarely 1–2 cm long; blade 4–8 by 2–4.5 cm, decurrent towards petiole, acute, upper side pubescent or becoming glabrous, lower side paler, with distinct nerves. *Inflorescences* with many short branchlets, scorpioid, dense, scarcely elongated in fruit, strigose to villos, ebracteate. *Calyx* nearly sessile, 3–3.5 mm long, not accrescent after flowering, lobes 5, free to the base, subulate-linear. *Corolla* lavender-purple, tube appressed strigulose, twice as long as calyx, limb 4–5 mm in diam., lobes glabrescent, rounded. *Stamens*: anthers subsessile, crested dorsally by a wavy, antrorse trichome. *Pistil*: style longer than stigma. *Nutlets* 4, pitted, ellipsoid.

Distribution — Peru. Widely cultivated in tropical and temperate countries. *Malesia*: cultivated in Java and possibly elsewhere.

3. *Heliotropium brevifolium* Wall.

Heliotropium brevifolium Wall. in Roxb., Fl. Ind., ed. Carey & Wall., 2 (1824) 2. — *Heliotropium strigosum* Willd. var. *brevifolium* (Wall.) C.B. Clarke in Hook. f., Fl. Brit. India 4 (1885) 151. — Type: Wallich Cat. 914 (K holo).

Perennial or annual, decumbent herb. Stems 3–10(–15) cm long, branched mainly in the inflorescence, covered by stiff, antrorsely appressed hairs. *Leaves* sessile, linear, horizontally arranged left and right from the stems, 4–10 by 0.8–1 mm, tapering towards base, acute, with revolute margins, both sides with antrorse, appressed hairs. *Inflorescence* 0.5–3 cm long, spike-like, with 3–12 flowers; bracts similar to leaves, the lowermost excluded shorter than the calyx; pedicels 0.5–0.8 mm long. *Calyx* 1.8–2 mm long in flower, 2.5 mm in fruit, lobes free to base, 0.8 mm wide, subacute, hairs as in the leaves. *Corolla* campanulate, white, 2.5 mm long, hairy outside, tube shorter than calyx, lobes broadly ovoid, rounded. *Stamens*: anthers subsessile, included in the tube. *Pistil*: style a little shorter than stigma; stigma conical from a discoid base, with minute papillae. *Nutlets* 1–1.1 mm high, ovoid, smooth, very densely covered by appressed hairs.

Distribution — India, ?Nepal; *Malesia*: Philippines (Luzon).

Note — The distribution is not yet clear, as *H. brevifolium* has not been recognized as a species separate from *H. strigosum* by many authors. It seems to be most common

in the Philippines, where the greatest number of herbarium specimens comes from, but there are also collections from northern India. Whether there is really a gap between this area and the Philippines seems doubtful.

Already Johnston [J. Arnold Arbor. 32 (1951) 113] pointed out several differences between African and Asian collections of *H. strigosum*. Nevertheless, *H. brevifolium* seems to be different also from the Asian plants mentioned under this name, as, for instance, Johnston describes the ovary as glabrous. In the Malesian area, *H. paniculatum* R.Br. has often erroneously been identified as *H. strigosum*, but Johnston's plants are different from that either.

According to Clarke in Hooker f. (1885), *H. brevifolium*, which he assigns the rank of a variety, is more common throughout India than true *H. strigosum*. Further investigations based on material from all the south-eastern Asian countries are necessary to define species and their area of distribution more exactly.

4. *Heliotropium curassavicum* L.

Heliotropium curassavicum L., Sp. Pl. (1753) 130; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 695; Backer & Bakh. f., Fl. Java 2 (1965) 461. — Type: *Herb. Cliff. 45* (BM), 'Habitat in Americae calidioris maritimis'.

Annual, prostrate to ascending, more or less succulent herb. Stems much branched, 5–50 cm or more long, glabrous. *Leaves* shortly stalked to sessile, oblong, spatulate, lanceolate to linear, glaucous, 1–5 by 0.3–1 cm, glabrous. *Cymes* spike-like, 3–10 cm long, dense, ebracteate, usually forked once. *Calyx* subsessile, short, cleft to the base into 5 linear, acute lobes, glabrous. *Corolla* 1–2.5(–3) mm long, white or bluish with a yellow centre, tube broadening towards base, longer or equalling the calyx, lobes 5, rounded. *Stamens*: anthers subsessile, sagittate, mucronate at apex. *Pistil*: style indistinct, stigma 0.2 mm long, with a broad, discoid base. *Fruit* breaking up into 4 nutlets; nutlets 1.6–1.8 mm long, wedge-shaped, smooth at first, later sometimes rugulose, glabrous.

Distribution — A native of the Americas from Patagonia to the United States and the West Indies; *Malesia*: occasionally occurring as a weed in widely different places such as Java (near Bogor) and the Philippines.

Habitat — In its native countries in wet places, along the sea shore, etc.

5. *Heliotropium elongatum* (Lehm.) Cham.

Heliotropium elongatum (Lehm.) Willd. ex Cham., Linnaea 4 (1829) 452; Backer & Bakh. f., Fl. Java 2 (1965) 462. — *Tiaridium elongatum* Lehm., Pl. Asperif. Nucif. (1818) 16. — Type: not indicated. *Heliotropium decipiens* Steenis ex Backer, nomen in Backer & Bakh. f., Fl. Java 2 (1965) 462, in syn.

Annual herb up to 60 cm high. Stem simple or with 1 or 2 branches, with few patent, white, bristly hairs and short hairs. *Leaves*: petiole 1.5–4 cm long; blade ovate, 2.5–8 (–10) by 1.5–6 cm, base horizontally truncate, long decurrent, apex acute, with 4–5 primary nerves on each side and a network of nerves of higher order, short strigillose on upper, appressed hairy with longer bristles along main nerves on the lower side. *In-*



Fig. 7. *Heliotropium indicum* L. Flowering twig. Pontianak, weed in garden. Photo A. Elsener, 1961.

florescence simple, spike-like, elongate, ebracteate. *Calyx* sessile, 2–2.5 mm long, with longer and shorter patent hairs, cleft to the base into 5 linear, acute lobes 0.5 mm wide. *Corolla* salver-shaped, tube 4.5–5 mm long, limb c. 3 mm in diam., first purple, then pale yellowish with a darker centre, at last purple again, lobes rounded, c. 1 mm long. *Stamens*: anthers subsessile at about the middle of the tube. *Fruit* shallowly two-lobed with margins of lobes meeting each other above middle of fruit, parting into 2 two-locular halves.

Distribution — A native of South America; in *Malesia* naturalized in parts of Java (from Bogor to Depok in the West, near Malang and Puger in the East).

Habitat — No data available.

6. *Heliotropium indicum* L.

Heliotropium indicum L., Sp. Pl. (1753) 130; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 695; Ridl., Fl. Malay Penins. 2 (1923) 441; I.M. Johnston, J. Arnold Arbor. 32 (1951) 111; Backer & Bakh. f., Fl. Java 2 (1965) 462; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 94. — Type: probably in *Herb. Cliff.* (BM), 'Habitat in India utraque'.

Annual herb 15–60 cm high. Stem simple or with few branches, with few patent, bristly hairs and shorter, irregularly directed or retrorse hairs. *Leaves*: petiole 1–9 cm long; blade ovate, (1.5–)2–10(–12) by 0.8–8(–9) cm, base horizontally truncate, long decurrent, apex acute, primary nerves 4–7 on each side, between them a dense network of nerves of higher order, upper side with bristles arising from white tubercles of mineralized cells and short hairs, lower side with dense, white tubercles of mineralized cells and bristly hairs along the nerves. *Inflorescence* spike-like, elongate, cymes 1 to several, 5–20 cm long, ebracteate. *Calyx* sessile, 1.5–2 mm long, with patent, white, bristly hairs, lobes free to base, less than 0.5 mm wide, acute. *Corolla* salver-shaped, with appressed white hairs outside, tube 3–4.5 mm long, limb pale violet, blue or white, throat sometimes orange-yellow, lobes rounded, c. 1 mm long. *Stamens*: anthers subsessile at about middle of tube. *Pistil*: style slightly longer than stigma, the stigma short conical, broadly obtuse. *Fruit* 2–3 mm long, deeply bifid, margins of lobes meeting far below middle of fruit or at very base only, apices divergent, fruit-halves two-celled, cells two-locular, outer partition with one seed, inner one larger, empty. — **Fig. 7.**

Distribution — Probably a native of tropical America, now widespread in all the tropical regions of the world; *Malesia*: Sumatra, Malay Peninsula, Singapore, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands (Lombok, Sumbawa, Sumba, Flores, Timor), Moluccas, New Guinea.

Habitat — Waste lands, botanical gardens, close to ponds, in disturbed areas, etc.

7. *Heliotropium madurense* Riedl

Heliotropium madurense Riedl, Blumea 38 (1994) 463. — Type: *Backer 20943* (L. holo), Madura. *Heliotropium paniculatum* auct. non R. Br.: Backer & Bakh. f., Fl. Java 2 (1965) 462.

Annual, 6–35 cm high. Stems reddish brown, branched mainly in the upper half but with few branches often also from near base appearing at a later stage, with short, an-

trorsely appressed hairs. *Leaves* sessile, soon evanescent, linear, 0.7–1.5 by c. 0.1 mm, tapering towards base, apex subacute to obtusish, midrib deeply impressed, no lateral nerves present, margins revolute, covered by antrorse, bristly hairs on lower side arising from one circle of mineralized cells, white incrustations sometimes also present along margins. *Inflorescence* spike-like; lower bracts 2.5 mm, upper ones 1.5 mm long; pedicels 1–1.2 mm long at least in fruit, arising at about 2–3 mm distance from each other, divaricate to suberect. *Calyx* 1.5 mm long, with few appressed, bristly hairs, lobes free to base, ovate, 0.8 mm wide, subobtus. *Corolla* funnel-shaped, white, 1.8–2 mm long, 1.5 mm in diam., white-powdery with bristly hairs outside, tube as long as calyx, lobes ovate to obovate, subvalvate in bud, 0.8 mm long. *Stamens*: anthers subsessile in upper part of tube, ovate. *Pistil*: style 0.3 mm long, stigma 0.4 mm with a broad disc and a central, obtuse cone. *Fruit* separating into 4 nutlets, constricted at margins of nutlets, 1 mm high, white-powdery on surface. — **Fig. 8.**

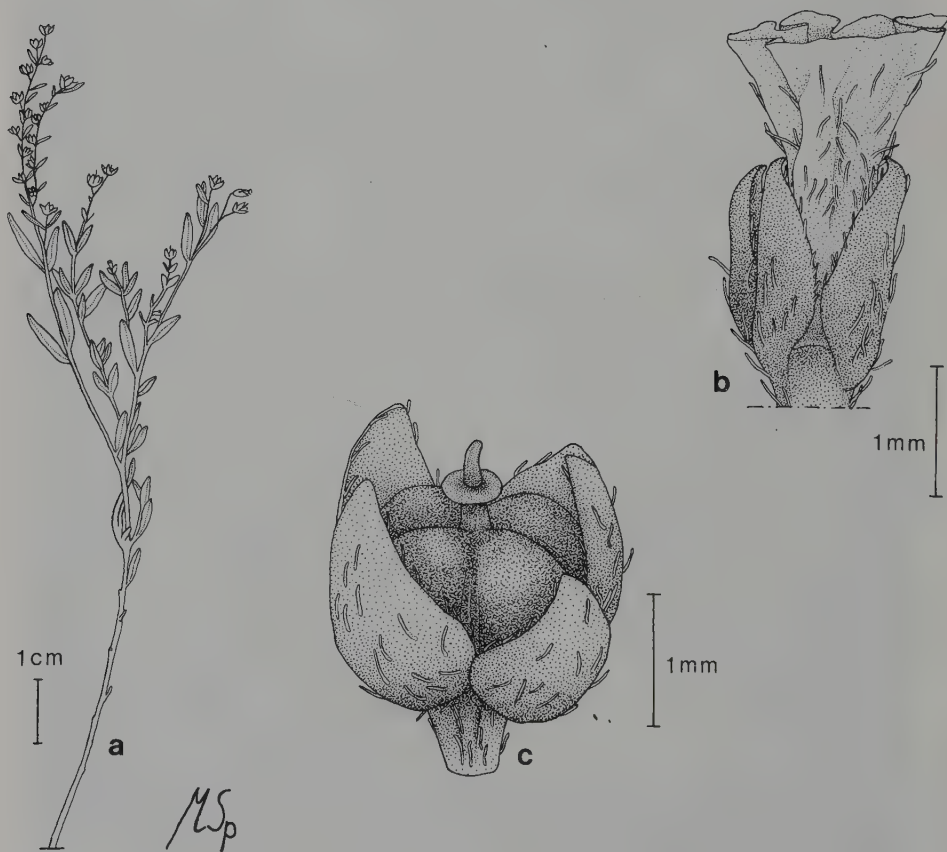


Fig. 8. *Heliotropium madurense* Riedl. a. Top of flowering branch; b. flower; c. fruit in calyx (Backer 20943). Drawing M. Spitteler.

Distribution — *Malesia*: endemic to Madura.

Note — The specimens seen are obviously identical with what Backer & Bakhuizen van den Brink (1965) called *H. paniculatum*. These authors also mention as only occurrence the island of Madura.

8. *Heliotropium ovalifolium* Forssk.

Heliotropium ovalifolium Forssk., Fl. Aegypt.-Arab. (1775) 38. — Type: *Forsskål s.n.* (C holo), Yemen, Hadie.

Perennial herb, sometimes with woody base. Stems up to 40 cm high, much branched, covered by antrorsely appressed, short hairs. *Leaves*: petiole 1–5 mm long; blade oblong-obovate, 10–15 by 3–4 mm, tapering gradually towards base, apex obtuse, rarely subacute, nerves indistinct, hairs on both sides white, silky, antrorse, sometimes a little patent. *Inflorescence* a spike-like, ebracteate cyme, flowers more or less dense, arranged in two ranks; pedicels usually less than 0.5 mm. *Calyx* 2 mm long, cleft to the base, covered densely by antrorse hairs, lobes 0.5–0.6 mm wide, slightly unequal. *Corolla* funnel-shaped, white, 3 mm long, 2 mm in diam., with dense, antrorse hairs outside, lobes ovate-triangular to ovate, 0.8 mm long. *Stamens*: anthers subsessile at middle of tube. *Pistil*: stigma sessile or subsessile, conical from a wider base. *Nutlets* 4, ovoid, densely antrorse hairy.

Distribution — Tropical Africa, Arabian Peninsula, India, Vietnam, Solomon Islands; *Malesia*: Lesser Sunda Islands (Sumba, Timor).

Habitat — In valleys, on road sides, in dried pond, etc.

9. *Heliotropium paniculatum* R.Br.

Heliotropium paniculatum R.Br., Prodr. Fl. Nov. Holl. 1 (1810) 494. — Type: *R. Brown s.n.* (K holo), tropical Australia.

Perennial, sometimes with woody base, (10–)15–40 cm high. Stem much branched, branches upright to divaricate, stem and branches covered by long, appressed, bristly hairs. *Leaves* sessile, linear to linear-subulate, (0.7–)0.8–2.5(–3) cm long, c. 1 mm wide, base attenuate, apex acute, margin revolute, both sides covered by long appressed bristly hairs. *Cymes* elongate; bracts linear, 3–4 mm long; pedicels 0.5–1 mm long. *Calyx* c. 2.2 mm long, hairs as on leaves, lobes free to the base, lanceolate, acute, 0.8 mm wide. *Corolla* funnel-shaped, white, 2.5–3.3 mm long, 1.5–2 mm in diam., outside with few hairs, tube shorter than calyx, lobes rounded, 0.7–0.8 mm long. *Stamens*: anthers subsessile in tube. *Pistil*: style 1.5–3 times as long as stigma, stigma subulate from a discoid base. *Fruit* separating into 4 nutlets, nutlets ovoid, 0.8–1 mm high, covered with very short, appressed hairs.

Distribution — Australia; *Malesia*: ?Lesser Sunda Islands (Flores, a very untypical specimen, that cannot be assigned to the present species with certainty), New Guinea.

Notes — 1. The species is flowering already in the first year and can, therefore, be mistaken for annual.

2. The plants from Madura under this name belong to *H. madurensse*. The specimens from New Guinea have mostly been misidentified as *H. strigosum*, which does not seem to occur in the Malesian region.

10. *Heliotropium scabrum* Retz.

Heliotropium scabrum Retz., Observ. 2 (1781) 8. — Type: not indicated.

Heliotropium marifolium Retz., l.c.; Backer & Bakh. f., Fl. Java 2 (1965) 462. — Type: Koenig.

Heliotropium cyrtostachyum Miq., Fl. Ind. Bat. 2 (1856) 924. — Type: Horsfield, Java.

Perennial. Stems prostrate, 5–30 cm long, branched from the base, upper branches very short, covered with antrorsely appressed, white, bristly hairs. *Leaves*: petiole 0–3 mm long; blade linear to lanceolate or lanceolate-oblong, 5–20 by 1–5 mm, base either narrow or rounded, apex acute, margin revolute, hairs as on stem on both sides. *Cymes* subcapitate at end of stems and branches, with leaf-like bracts; pedicels up to 1 mm long. *Calyx* 2.5–3 mm long, lobes free to the base, lanceolate to triangular-lanceolate or ovate-lanceolate, acute, 0.6–0.7 mm wide in flower, up to 1.2 mm in fruit, hairs as in stem. *Corolla* funnel-shaped, white, sometimes with a yellow eye, 3–3.5 mm long, outside covered with stiff hairs, tube much shorter than calyx, lobes ovate-oblong, with wavy margin, 1–1.2 mm long. *Stamens*: anthers subsessile in tube, ovate-oblong, acute, 0.6 mm long. *Pistil*: style 0.4 mm long, stigma slightly longer than style. *Fruit* separating into 4 nutlets, nutlets 1.8–2 mm long, 1.4–1.5 mm wide, ovoid-acute, covered dorsally with short, dense, more or less patent hairs.

Distribution — Pakistan, India, Sri Lanka, Cambodia, Hainan; *Malesia*: Java, Celebes? (identification highly uncertain), Lesser Sunda Islands (Flores). Johnston's (1951) assumption that it also occurs on New Guinea could not be verified.

Habitat — In dunes.

11. *Heliotropium ventricosum* R.Br.

Heliotropium ventricosum R.Br., Prodr. Fl. Nov. Holl. 1 (1810) 494. — Type: *R. Brown s.n.* (K holo), tropical Australia.

Annual herb. Stem erect, 5–18 cm high, with numerous short, erect branches, with white, more or less patent or appressed hairs. *Leaves* sessile, linear-lanceolate, needle-like, 0.5–1.8 by c. 1 mm, tapering towards base, acute, with revolute margins, hairs dense, white on both sides as in stem. *Cymes* with densely crowded flowers, 1.5–2.5 cm long; bracts leaf-like, longer than calyx; pedicels less than 1 mm. *Calyx* cleft to the base into slightly unequal lobes, 4 lobes 3.5 mm, the fifth 4 mm long, 0.8–1 mm wide, sharply acute, with hairs as in leaves. *Corolla* white, hairy as calyx outside, 4.5–5 mm long, 2.5–3 mm in diam., tube very narrow, strongly inflated above middle by the anthers, lobes elliptical to ovate, 1.2 mm long, curved inwards when young. *Stamens*: anthers subsessile, ovoid, 0.5–0.6 mm long, inserted at about 2/3 of length of tube above base. *Pistil*: style long, filiform in upper part, breaking after flowering above

conical base that is persistent in fruit; stigma short conical. *Fruit* breaking up into 4 nutlets; nutlets short-ovoid, covered with very short, appressed hairs in upper part.

Distribution — Australia; *Malesia*: Lesser Sunda Islands (Timor), Moluccas (Aru), New Guinea.

DOUBTFUL SPECIES

Heliotropium orientale L., Sp. Pl. (1753) 131. — *Lithospermum javanicum* Spreng., Syst. Veg. 1 (1825) 547, nom. illeg.

Annual. Leaves linear, glabrous, without veins, with few lateral flowers.

Note — The species is based on a collection of Houttuyn from Java (Linnaeus only mentions 'Asia'). It seems to be a glabrescent specimen of *Heliotropium scabrum* Retz., and certainly not a member of *Lithospermum*, as Sprengel suggested.

MYOSOTIS

Myosotis L., Sp. Pl. (1753) 131; Gen. Pl., ed. 5 (1754) 165; Stroh, Beih. Bot. Centralbl. 61B (1941) 317; Grau & Leins, Ber. Deutsch. Bot. Ges. 81 (1968) 107; Grau & Schwab, Mitt. Bot. Staats-samml. München 18 (1982) 9. — Type species: *Myosotis scorpioides* L.

Perennial, biennial or annual herbs with alternate, lanceolate, oblanceolate or oblong leaves. Basal *leaves* stalked, stem leaves usually sessile or nearly sessile. *Inflorescence* scorpioid or terminated by a single flower, usually without bracts. *Calyx* on a distinct pedicel, with 5 lobes not free to the base, with straight or hooked appressed or spreading hairs, rarely almost glabrous. *Corolla* rotate or rarely campanulate, usually blue or white, limb 5-lobed, lobes spirally arranged in bud, overlapping marginally; scales (for-nices) always present in the throat. *Stamens* with distinct filaments and anthers, that often have a rounded apical, more or less hood-shaped, hyaline appendix. *Ovary* 4-lobed, stigma either distinct, cushion-shaped, or indistinct, club-shaped. *Nutlets* 4, compressed ovoid, smooth, shiny, in the upper part with or without a flat, narrow keel-like margin; areola minute, basal to subbasal, attached to the flat receptacle, with or without caruncula. *Pollen* 3- to 5-colporate, with distinct sculptured areas. — **Fig. 9, 10.**

Distribution — More than 100 species, most common in temperate and subarctic regions of the Old World, but also in the tropics at higher altitudes, section *Exarrhena* with its centre in New Zealand. A few species are also found in temperate North America, one species in Patagonia.

Habitat — Many species grow under humid conditions and there are scarcely any xerophytic groups, but otherwise occurring in a great variety of habitats.

Notes — 1. The genus is unique within the whole family by the spiral arrangement of the corolla lobes in bud. Another unusual feature is the sterile apical appendix of the anthers that consists of several layers of hyaline cells beyond the end of the vascular bundles. It is covered by the epidermis continuous with the rest of the anther and may

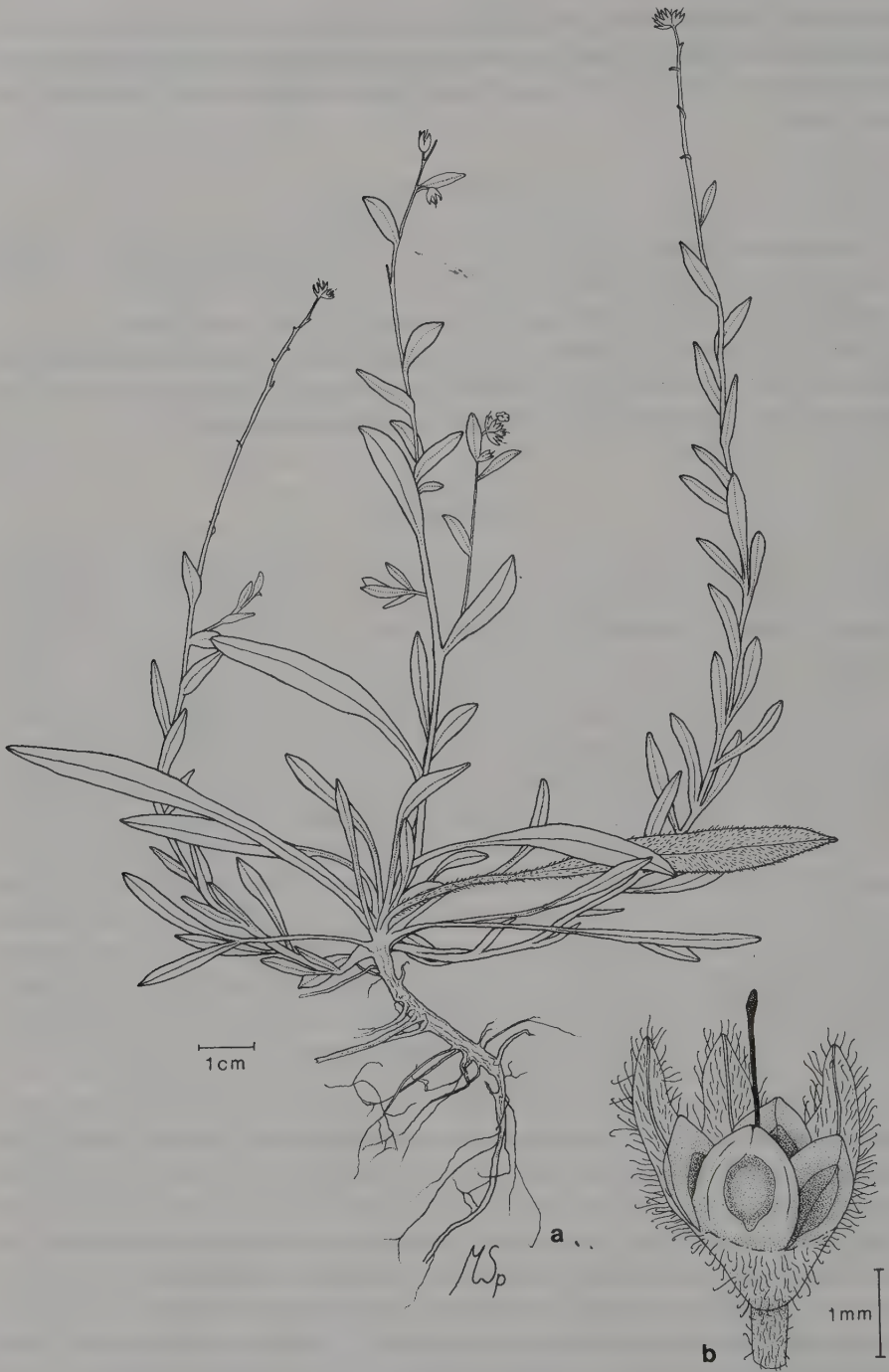


Fig. 9. *Myosotis australis* R. Br. a. Plant in flower; b. fruits in calyx (Stevens & Coode LAE 54511). Drawing M. Spitteler.

be either semicircular and dome-like or nearly ovoid and longer than wide. Its shape seems to offer a reliable distinctive character for various groups within the genus (Grau & Schwab 1982). Over-all shape as well as length and distribution of papillae of scales and stigma are likewise criteria of importance for systematics and lead to similar groups.

2. There are two distinct types of pollen size. Large-sized pollen is characteristic for species of the southern hemisphere together with the *M. discolor* group in the northern. It seems best suited to characterize section *Exarrhena* in a natural way.

3. Polyploidy is frequent on the basic numbers $x = 9, 10, 11, 12$. See A.A. Fedorov (ed.), Chromosome numbers of flowering plants (1969) 160.

Taxonomy — As said above, *Myosotis* holds a very isolated position within the *Boraginaceae* and is best taken as the only member of the monotypic tribe *Myosotideae* Rchb. Closest affinities seem to be with *Trigonocaryum* formerly included in *Myosotis* as sect. *Phyllocephalum* Boiss., and probably also with *Trigonotis*.

Strophostoma DC. was kept as a separate section for the presence of a distinct caruncula, which is a difference in quantity, not in quality, however, as there are small similar structures found also in other groups. At present, only two sections are discerned by authors such as Grau & Schwab (1982). I follow their descriptions here.

Section *Myosotis*: Stigma with small, well differentiated papillae, usually bilobed. Pollen grains small. Scales in corolla throat with long papillae: *M. scorpioides* L.

Section *Exarrhena* DC.: Stigma with large, clavate papillae, usually simple. Pollen grains large. Scales in corolla throat short: *M. australis* R.Br.

Uses — *Myosotis* spp. are frequently grown as ornamentals.

KEY TO THE SPECIES

- 1a. Hairs of calyx spreading, mostly hooked at apex **1. *M. australis***
- b. Calyx covered by straight, appressed hairs **2. *M. scorpioides***

1. *Myosotis australis* R.Br.

Myosotis australis R.Br., Prodr. Fl. Nov. Holl. (1810) 494; Van Royen, Pac. Sc. 29 (1975) 80; Alpine Fl. New Guinea 4 (1983) 3090. — Type: *R. Brown* (K), Australia, Port Jackson.
Myosotis saruwagedica Schltr. ex O. Brand in Diels, Bot. Jahrb. 62 (1929) 490. — Type: *Keysser 21* (B, destroyed), New Guinea, Saruwaged Mts.

Perennial herb. Stems arising either round a central rosetta of leaves or at the end of long, subterranean, creeping runners, ascendent, 10–40 cm high, simple or with 1 or 2 branches, hairs spreading in lower, more or less antrorse in uppermost part. *Leaves* oblong, spatulate-oblong or lanceolate-oblong, petiole winged, 1–4(–6) cm long in rosetta leaves, 0–0.5 cm in stem leaves, blade 5–10 by 0.5–1.2 cm in rosetta leaves, 2.5–3.5 by 0.3–0.8 cm in lower, 0.8–2 by 0.3–0.5 cm in upper stem leaves, tapering towards base, obtuse to subacute, hairs denser, antrorse or irregular, arising from a group of mineralized cells or not on lower, looser except on midrib, antrorse or slightly irregular, rarely spreading on upper side. *Inflorescence* short, indistinctly scorpioid first,



Fig. 10. *Myosotis australis* R. Br. Flowering plants (van Royen 30020). Murray Pass, Papua New Guinea. Photo P. van Royen, 1965.

strongly elongated, fairly straight later on, rhachis with antrorse hairs sometimes hooked at apex, ebracteate; pedicels 1–2 mm long, hairy. *Calyx* campanulate, 2–2.5 mm long in flower, 3–4 mm soon afterwards, deciduous with nutlets, divided to 4/5 into lanceolate, 0.5–0.8(–1) mm wide, subacute to obtusish lobes; hairs near base reflexed-spreading, others spreading, with hooked apex especially in lower part of calyx, but sometimes in its whole length. *Corolla* funnel-shaped, white to pink, yellowish, bluish, 3.5–4 mm long, about 3 mm in diam., tube 2.5–3 mm long, lobes rounded orbicular, 1–1.5 mm in diam., glabrous; fornicies kidney-shaped, yellow. *Stamens*: anthers subsessile, oblong, sometimes apiculate, 1.5 mm long. *Pistil*: style 2.5–4 mm long, filiform, stigma small, clavate. *Nutlets* ovate in outline, compressed, 1.5 mm long, 1 mm wide, in upper part with a flat, broadly obtuse rim, smooth, shining. — **Fig. 9, 10.**

Distribution — New Zealand, Tasmania, temperate Australia; **Malesia**: mountains of New Guinea.

Habitat — Montane to alpine altitudes, in wetter part of grasslands, landslides, deserted gardens (according to Van Royen).

Notes — 1. *Myosotis saruwagedica* has been separated from *M. australis* mainly for differences in the indument. It should have longer, soft hairs especially along the margin. This difference does not hold, when more numerous specimens are compared. Even plants from the Saruwaged mountains do not show the typical characters. No other distinguishing characters could be found.

2. The most obvious peculiarity of the species in the wide sense is the deciduous calyx. In older plants, there are only the pedicels remaining in the lower part of the cymes.

3. According to Grau & Schwab (1982), *M. australis* has pollen grains characterized by a rhomboidal area on the colpi and only loosely verruculous surface, while the rhomboidal area is less distinct and wartlets are dense in the otherwise closely related *M. saruwagedica*. As no correlations to other characters could be found, the value of this difference seems to be rather doubtful.

2. *Myosotis scorpioides* L.

Myosotis scorpioides L., Sp. Pl. (1753) 131; Backer & Bakh. f., Fl. Java 2 (1965) 464. — Type: *Herb. Cliff.* 46 (*β palustris*) (BM).

Perennial with a creeping rhizome, often stoloniferous. Stem erect or ascendent, 15–45 cm high, angular, more or less hairy. Lower leaves 4–7 cm long, oblong-lanceolate to obovate-lanceolate, subobtusate, tapering towards base, usually sessile, nearly glabrous or with few appressed hairs; the upper leaves narrowly oblong, often apiculate, smaller. Cymes without bracts, single or bifurcate; fruiting pedicels as long as to twice as long as the calyx, spreading (especially in upper flowers) or reflexed. Calyx campanulate, 2.5–3 mm long in flower, 4–5 mm in fruit, covered by appressed hairs, cleft to 1/3 or 1/2 into triangular teeth. Flowers female or hermaphroditic, distinctly larger in the first case, salver-shaped with a short tube included in the calyx, limb rotate, explanate, 4–10 mm in diam., first pink, later sky-blue, rarely white, lobes rounded-emarginate; fornicies yellow. Stamens: anthers lanceolate, included in the corolla. Pistil: style about as long as tube of calyx or surpassing the calyx in length. Nutlets narrowly ovate in outline, obtuse, 1.5 mm long, 1 mm wide, with a narrow, flattened border, black, shining.

Distribution — Nearly all Europe, Asia south to N India, N Africa, N America; *Malesia*: introduced in Java and, maybe, other parts of the Malesian area.

Habitat — Often cultivated, especially in mountain areas.

OMPHALODES

Omphalodes Moench, Meth. (1794) 419; Brand in Engl., Pflanzenr., fam. IV.252 (1921) 96. — Type species: *Cynoglossum omphalodes* L. [= *Omphalodes verna* Moench].

Perennial herbs, often with a creeping rhizome, or annuals. Leaves alternate, basal leaves and leaves of sterile creepers often different in shape from stem leaves. Flowers solitary in the axils of upper leaves or in loose, raceme-like cymes, usually without bracts, pentamerous. Calyx-lobes free to the base. Corolla cylindrical-campanulate or more often rotate with a short tube and spreading limb; scales in the throat well devel-

oped. *Stamens*: anthers nearly sessile, ovoid. *Pistil*: style shorter than the calyx, usually with a cushion-shaped stigma. *Nutlets* umbilicate dorsally, attached to the small, pyramidal receptacle and surpassing it in length several times, depressed globose to ovoid, with an incurved, entire or toothed margin; embryo straight or rarely curved.

Distribution — About 25 species mainly in the Mediterranean region, Mexico and China, but with few species in Central Europe, Caucasus, etc. *Omphalodes linifolia* is widely cultivated and sometimes escapes from culture.

Note — Basic chromosome numbers seem to be $x = 6, 7, 11$, but no diploids are known apart from one species with $2n = 22$.

***Omphalodes linifolia* (L.) Moench**

Omphalodes linifolia (L.) Moench, Meth. (1794) 419; Backer & Bakh. f., Fl. Java 2 (1965) 463. — *Cynoglossum linifolium* L., Sp. Pl. (1753) 134. — Type: *Herb. Cliff.* (BM)

Annual; stem slender, 8–30 cm high, simple or branched, slightly angulate. Basal leaves stalked, cuneiform, stem leaves linear to lanceolate, rarely ovate, 1–5 by 1–1.6 cm, margin ciliate, surface glabrous on both sides, sometimes with small tubercles of mineralized cells. *Cymes* elongate, without bracts or with one or two bracts at the very base, loose; pedicels much longer than calyx, horizontally spreading at last. *Calyx* 3 mm long in flower, 4–4.5 mm in fruit, cleft to the base into lanceolate-subulate, ciliate lobes. *Corolla* white, rarely bluish, 5.5–7.5 mm long, 8–13 mm in diam., limb divided to middle into rounded lobes; fornicies nearly trapeziform. *Pistil*: style very short. *Nutlets* depressed globose, 4 mm in diam., ciliate, crenate-dentate at margin, with a large umbilicus.

Distribution — Southern France, Portugal, Spain; *Malesia*: introduced in Java in cultivation.

Note — No specimens from the Malesian area could be examined. The description is taken from Brand in Engler, Pflanzenreich. According to Backer and Bakhuizen van den Brink, l.c., the plants from Java belong to var. *obtusata* DC., Prodr. 10 (1846) 161 and are described a little different in some details: Plants 15–60 cm high. Leaves elongate-spathulate, 2–10 cm long, 0.25–1.5 cm wide, glaucous, rough from few, scattered hairs. *Calyx* 4–5 mm long at flowering time, strongly accrescent, with spreading lobes, up to 1.5 cm across. *Nutlets* ovoid, 4.5–5 mm long, acutely keeled.

ROTULA

Rotula Lour., Fl. Cochinch. (1790) 121; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 693; I.M. Johnston, J. Arnold Arbor. 32 (1951) 14. — Type species: *Rotula aquatica* Lour.
Rhabdia Mart., Nov. Gen. 2 (1827) 136, t. 195; Vidal, Rev. Pl. Vasc. Filip. (1886) 194; Ridl., Fl. Malay Penins. 5 (1925) 323. — Type species: *Rhabdia lycioides* Mart. [= *Rotula aquatica* Lour.].

Shrub with several slender, ascending to prostrate, virgate stems. *Leaves* small, subcoriaceous, sessile or subsessile, on short lateral branchlets. *Inflorescence* a small cyme

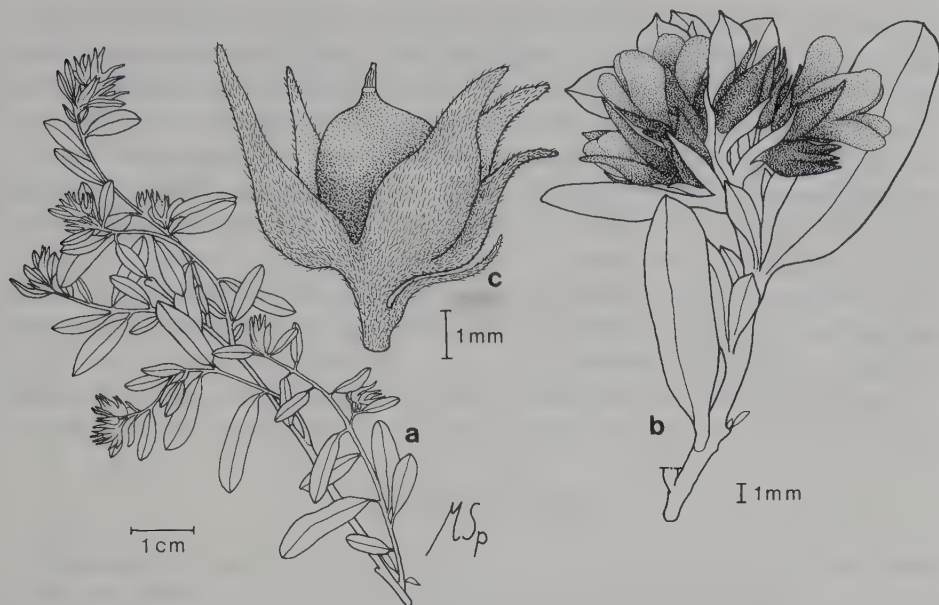


Fig. 11. *Rotula aquatica* Lour. a. Habit of twig; b. inflorescence; c. fruit in calyx (van Steenis 19578). Drawing M. Spitteler.

terminating the branchlets and main branches. *Corolla* with a short tube included in the 5-lobed calyx, with 5 spreading, rounded lobes. *Stamens* exerted with filiform, elongate, glabrous filaments. *Pistil*: style apical, slender, undivided, with an indistinctly bilobed stigma. *Fruit* drupaceous, red, with a strongly 4-lobed endocarp breaking up into 4 single-seeded pyrenes at an early stage. — **Fig. 11.**

Distribution — A small genus of 2 (or 3) species occurring in SE Asia, W Africa and eastern Brazil.

Habitat — The species of *Rotula* are restricted to forested, tropical areas, where they grow in rocky, gravelly to sandy places along streams that are periodically inundated for shorter or even longer periods.

Note — Among the SE Asian woody members of *Boraginaceae*, *Rotula* is characterized by leafy short shoots markedly different from the virgate long shoots, similar to the situation in *Carmona*. Its most important distinguishing character from *Ehretia*, to which it is closely related, is the undivided style.

***Rotula aquatica* Lour.**

Rotula aquatica Lour., Fl. Cochinch. (1790) 121; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 693; I.M. Johnston, J. Arnold Arbor. 32 (1951) 15. — Type: not indicated.

Rhabdia lycioides Mart., Nov. Gen. 2 (1827) 136; Vidal, Rev. Pl. Vasc. Filip. (1886) 194. — Type: *Martius* (M?), Bahia.

Shrub with many elongate, terete shoots. *Leaves* crowded on numerous lateral short-shoots, subcoriaceous; petiole 0.5–3 mm long; blade 0.6–2.5 by 0.2–0.9 cm, oblanceolate to oblong, strigose or woolly strigillose, rarely glabrous, with indistinct nerves. *Inflorescence* a short, terminal, few-flowered cyme; pedicels in axils of bracts. *Calyx* 4–5 mm long, lobes unequal in width, 0.5–1.5 mm wide. *Corolla* pink to purplish, 5–7 mm long, tube 1–2 mm long, lobes rounded, explanate. *Stamens*: filaments attached above middle of corolla-tube. *Pistil*: style undivided, 4–5 mm long. *Fruit* red, drupaceous, subglobose, 3–4 mm in diam. — **Fig. 11.**

Distribution — Tropical Africa, India, Sri Lanka, southern China, Vietnam, Laos, Thailand, Burma; *Malesia*: Malay Peninsula, Borneo, Philippines, Celebes, New Guinea.

Habitat — See under the genus.

Uses — Medicinal use is recorded in Jansen et al. (eds.), *Plant Resources of SE Asia* (PROSEA Handb.), Basic List (1991) 244.

TOURNEFORTIA

Tournefortia L., *Sp. Pl.* (1753) 140; *Gen. Pl.*, ed. 5 (1754) 68; I.M. Johnston, *J. Arnold Arbor.* 16 (1935) 145; Backer & Bakh. f., *Fl. Java* 2 (1965) 460. — Type species: *Tournefortia hirsutissima* L. *Tetrandra* (DC.) Miq., *Fl. Ind. Bat.* 2 (1858) 928. — Type species: *Tetrandra wallichii* Miq. [= *Tournefortia tetrandra* Blume].

Messerschmidia L. ex Hebenstr., *Nov. Comm. Acad. Sci. Imp. Petrop.* 8 (1763) 315, t. 11; I.M. Johnston, *J. Arnold Arbor.* 16 (1935) 161; 32 (1951) 118; Backer & Bakh. f., *Fl. Java* 2 (1965) 461; Ng in *Tree Fl. Malaya* 4 (1989) 58. — Type species: unknown.

Argusia Boehm. in Ludwig, *Defin. Gen.*, ed. Boehmer (1760) 507; Dandy, *Reg. Veg.* 51 (1967) 28, 121; *Bot. J. Linn. Soc.* 65 (1972) 256; Heine in *Fl. Nouv.-Caléd.* 7 (1976) 108; Dayang Awa in *Tree Fl. Sabah & Sarawak* 2 (1996) 95. — Type species: *Argusia sibirica* (L.) Dandy [= *Tournefortia sibirica* L.].

Mallotonia (Griseb.) Britt., *Ann. Missouri Bot. Gard.* 2 (1915) 47; Heubl et al., *Bot. Jahrb.* 112 (1990) 154. — Type species: *Tournefortia gnaphalodes* R.Br.

Trees, shrubs (often scandent) or herbs. *Leaves* large or small, alternate or more rarely opposite, sometimes crowded apically on the branches, sessile with narrow base or stalked. *Inflorescences* terminal or lateral, usually dichotomously or trichotomously branched, composed of unilateral cymes without bracts. *Flowers* tetra- or pentamerous. *Corolla* with a short or elongate, cylindrical or sometimes campanulate tube and spreading lobes usually conduplicate in bud. *Stamens* included in the corolla, with very short filaments, sometimes mucronulate at apex. *Pistil*: style almost lacking, stigma with a fertile, basal ring and a sterile apical portion, often bilobed at apex. *Fruit* either a white drupe with juicy mesocarp (sect. *Tournefortia* and sect. *Tetrandra*) or dry, with a corky, vesicular mesocarp, endocarp breaking up into two 2-seeded or four 1-seeded pyrenes. — **Fig. 12, 13.**

Distribution — About 150 species, most of which are native in America, about 15 species in the Old World.

Habitat & Ecology — There are 4 species with corky mesocarp that are confined to coastal areas. Obviously, the special anatomy of the fruit is an adaptation to dispersal by water. Other groups are inhabitants of forested country or rocky places.

Uses — *Tournefortia argentea* is used as a vegetable and the fruits are sometimes also eaten and have antihistaminic properties. *Tournefortia sarmentosa* also has medicinal applications. See Heine in Fl. Nouv.-Caléd. 7 (1976) 110; Jansen et al. (eds.), Plant Resources of SE Asia (PROSEA Handb.), Basic List (1991) 201, 248.

Note — In most publications of more recent times, the genus *Tournefortia* is confined to species with fleshy endocarp, while those with corky endocarp are assigned to *Argusia* Boehm. (= *Messerschmidia* Hebenstr.) with the type species *A. sibirica* (L.) Dandy. *Argusia sibirica* from the coast of the Black Sea to the Pacific coast of Siberia and N China on one side has not much in common with *A. argentea* (L. f.) Heine from the eastern coast of Africa to Australia and Polynesia and *A. gnaphalodes* (L.) Heine from the West Indies (type species of *Mallotonia*) on the other. Either three genera have to be recognized or *Tournefortia* must be taken in a wide sense to include all three as sections. The present author prefers to adopt the latter solution of the problem.

KEY TO THE SPECIES

- 1a. Endocarp spongy. Trees **1. *T. argentea***
- b. Endocarp fleshy, fruit a drupe. Usually climbing shrubs 2
- 2a. Flowers tetramerous. Leaves paler on lower side, nerves forming a dark reddish brown pattern when dry **7. *T. tetrandra***
- b. Flowers pentamerous. Leaves not like that on lower side 3
- 3a. Leaves distinctly opposite. Flowers sessile 4
- b. Leaves alternate. Flowers sessile or shortly stalked 5
- 4a. Base of leaves cordate to horizontally truncate, or, if rounded, leaves lanceolate. Calyx lobes triangular to lanceolate-triangular, free for two thirds of their length **2. *T. luzonica***
- b. Base of leaves rounded, rarely obliquely truncate. Calyx lobes linear lanceolate, free for most of their length, at least for three quarters **5. *T. oppositifolia***
- 5a. Corolla only 2.5 mm long **3. *T. minutiflora***
- b. Corolla at least 5 mm long 6
- 6a. Flowers with a short pedicel. Fruit breaking up into 2 two-celled pyrenes. Leaves greyish tomentose on lower side **4. *T. muelleri***
- b. Flowers sessile. Fruit breaking up into 4 one-celled nutlets. Leaves not tomentose on lower side, the same colour as above or a little paler **6. *T. sarmentosa***

1. *Tournefortia argentea* L. f.

Tournefortia argentea L. f., Suppl. Plant. (1781) 133; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 693; Ridl., Fl. Malay Penins. 2 (1923) 440. — *Messerschmidia argentea* (L. f.) I.M. Johnston, J. Arnold Arbor. 16 (1935) 164; 32 (1951) 121; Backer & Bakh. f., Fl. Java 2 (1965) 461; Ng in Tree Fl. Malaya 4 (1989) 64. — *Argusia argentea* (L. f.) Heine in Fl. Nouv.-Caléd. 7 (1976) 109; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 95, f. 1. — Type: *Koenig*, Sri Lanka.

Tree or shrub, 1–10 m high. Branches greyish, densely covered by soft, greyish white hairs. *Leaves* crowded at apex of branches; petiole 5–25 mm long, winged; blade



Fig. 12. *Tournefortia argentea* L. f. Flowering plants. Photo from Flora Malesiana archives, origin unknown.

oblanceolate to obovate, 10–20 by 3–8 cm, with entire margin, base long tapering towards petiole, apex obtuse to broadly rounded, nerves more or less distinct, both sides greyish white tomentose. *Inflorescence* terminal, subcorymbose to paniculoid, branched several times successively in dichotomies, branches of last order scorpioid cymes, peduncle 5–15 cm long. *Flowers* numerous in two ranks, sessile. *Calyx* 1.5–2 mm long, tomentose from dense, appressed hairs outside, glabrous inside, with 5 triangular-lanceolate to suborbicular lobes. *Corolla* white to pinkish white, 3–4 mm long, 4–7 mm in diam., salver-shaped, tube campanulate, about as long as calyx, lobes ovate to orbicular, pubescent outside. *Stamens*: filaments inserted 0.4–0.8 mm above base of tube, anthers exerted for half their length. *Pistil*: stigma sessile, with 2 conical apices. *Fruit* depressed-globose, 5–8 mm in diameter, with spongy wall. — **Fig. 12.**

Distribution — Coasts of E Africa, across the Indian Ocean, Ryukyu, Taiwan, Hainan, Vietnam, northern Australia to Polynesia, New Caledonia; *Malesia*: Sumatra, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands (Bali, Lombok, Timor), Moluccas, New Guinea.

Habitat — Sandy beaches, etc.

2. *Tournefortia luzonica* I. M. Johnston

Tournefortia luzonica I. M. Johnston, J. Arnold Arbor. 16 (1935) 156. — Type: Adduru 237 (A, K), Luzon.

Creeper or liana. Branches dark reddish brown, with very dense, crispulate hairs. *Leaves* arranged strictly opposite; petiole 8–15 mm, blade ovate to oblong-lanceolate, 4–12 by 1.2–5.5 cm, entire, base horizontally truncate to subcordate, apex acute to acuminate, densely covered by subappressed, irregularly directed hairs on both sides or hairs sparse. *Inflorescences* terminal and axillary, composed of short, very dense cymes, branches of last order dichotomous, divaricate, not elongated in fruit. *Flowers* sessile, arranged in 2 ranks. *Calyx* 3–3.5 mm long (Johnston: 1–2.5 mm), covered by very dense, patent hairs, lobes 5, free to the base, linear, 0.6–0.7 mm wide. *Corolla* greenish, salver-shaped, 9–10 mm long, 3.5–4 mm in diam. (Johnston: 5 by 2–2.5 mm), densely appressed hairy outside, tube cylindrical, lobes ovate, rounded, 1.5 mm long. *Fruit* ovoid-globose, 2.5 mm long, 2 mm in diam. when dry, wall fleshy.

Distribution — *Malesia*: Philippines (Luzon), New Guinea (Biak I.).
Habitat — Mountainous regions.
Note — Johnston (1935) gives much smaller measurements (in brackets in the above description) for calyx and corolla than were found in material from Leiden. The identity, however, is clear from the strictly opposite leaves.

KEY TO THE SUBSPECIES

- 1a. Leaves greyish from dense, short hairs a. subsp. **luzonica**
- b. Leaves never greyish, subglabrous to scabridulous hairy 2
- 2a. Leaves only with very few hairs, shining, ovate to ovate-oblong or ovate-lanceolate c. subsp. **sublucens**
- b. Leaves scabridulous on upper, densely hairy along nerves on lower side, more or less lanceolate b. subsp. **angustissima**

a. subsp. **luzonica**

Greyish from dense short hairs. .
Distribution — Northern, East-central and Southern Luzon, New Guinea (Biak I.).

b. subsp. **angustissima** Riedl

Tournefortia luzonica I.M. Johnston subsp. *angustissima* Riedl, Blumea 41 (1996) 443. — Type: *Ridsdale 1477* (L. holo).
Distribution — Luzon, only known from type locality: prov. Zambales, Santa Cruz.
Ecology — On ultrabasic soils.

c. subsp. **sublucens** (I.M. Johnston) Riedl

Tournefortia luzonica I.M. Johnston subsp. *sublucens* (I.M. Johnston) Riedl, Blumea 41 (1996) 443. — *Tournefortia luzonica* var. *sublucens* I.M. Johnston, J. Arnold Arbor. 16 (1935) 157. — Type: *Ramos & Edaño 44553* (A, BM, K), Zambales Prov.
Distribution — West-central Luzon.

3. *Tournefortia minutiflora* Riedl

Tournefortia minutiflora Riedl, Blumea 41 (1996) 443. — Type: *Ivalaoa* UPNG 7752 (L holo; K, LAE, UPNG), Papua New Guinea, Gulf Prov.

Shrub with very long, rope-like branches resting upon each other (climbing shrub?). Branches dark purple-brown with short, white, conical hairs bulbous at base. *Leaves* alternate, petiole 1–2 cm long, blade (3–)6–14 by (1–)2–7 cm, ovate to ovate-oblong, shortly acuminate, rounded at base, glabrous and shining on upper, asperulous with short, stiff hairs along middle nerve on lower side like petiole, nerves 8–10 on each side. *Inflorescence* sublateral, repeatedly dichotomously branched, with asperulous axes; branches of last order bearing flowers in two rows on their whole length, scorpioid, 2.5–3 cm long. *Calyx* sessile, 1–1.2 mm long, shortly patent-hairy, divided into short, lanceolate, acute lobes in its distal half. *Corolla* 2.5 mm long, folded longitudinally in juvenile state, salver-shaped, densely, more or less appressed hairy outside, tube nearly cylindrical, 2 mm long, limb up to 1.5 mm wide, with very short, acute lobes. *Fruit* not seen.

Distribution — Papua New Guinea, only known from the type collection.

Habitat — Tidal regrowth.

4. *Tournefortia muelleri* I.M. Johnston

Tournefortia muelleri I.M. Johnston, J. Arnold Arbor. 16 (1935) 157. — *Tournefortia mollis* F. Muell., Fragm. 1 (1858) 59, nom. illeg., nec Bertoloni (1852). — Type: *F. von Mueller* (K iso), Australia, Burdekin R.

Shrub or subshrub, 1–2.5 m high. Branches reddish brown, with dense, white, short, patent hairs. *Leaves*: petiole 5–25 mm long; blade ovate-lanceolate, ovate or rarely lanceolate, 2.5–10 by 1–6.5 cm, margin entire, base oblique to horizontally truncate, sometimes slightly decurrent in petiole, apex acute, acuminate or rarely obtuse, nerves impressed above, prominent below, upper side slightly rough from few appressed stiff hairs, lower side densely soft tomentose. *Inflorescence* composed of 3–5 more or less distinctly stalked cymes on 2 or 3 dichotomies, not much elongated after flower, terminal or lateral, with numerous sessile flowers in 2 ranks. *Calyx* campanulate, 2.5 mm long, 1.5 mm wide, densely strigulose outside and inside, lobes lanceolate from a wider base, 0.7–0.8 mm wide, acute, free to base. *Corolla* salver-shaped, white, 5–8 mm long, 3.5(–4) mm wide, densely strigulose outside, tube cylindrical, lobes ovate-oblong, rounded, entire, 1.2 mm long. *Stamens* inserted at or above middle of tube. *Pistil*: stigma subsessile, conical. *Fruit* depressed-subglobose to subglobose-pear-shaped, 2.5 mm long and wide or 2.7 mm wide when dry, wall fleshy.

Distribution — Northern Australia; *Malesia*: ?Java (Merapi), Philippines, Lesser Sunda Islands (?Bali, Sumba), New Guinea. In the case of Java, only Merapi is mentioned on the label, but no particular island. In the case of Bali, the identification is a little doubtful.

Habitat — Along rivers and in tidal area.

5. *Tournefortia oppositifolia* Riedl

Tournefortia oppositifolia Riedl, *Blumea* 41 (1996) 444. — Type: *van Balgooy 4885*, Moluccas, Buru.

Climber. Young twigs, petioles, leaves and inflorescence nearly glabrous or with a few, rarely more numerous hairs. Branches dark brown, finely longitudinally sulcate. Apart from the two uppermost ones *leaves* opposite or subopposite, ovate to ovate-lanceolate; petiole 5–20 mm long, sometimes flexuous as if used to attach to some minor branches; blade 3–10 by 1.5–5.5 cm, acuminate, broadly rounded at base, subglabrous or more or less densely short hairy especially on lower side, with 6 to 7 primary nerves on each side. *Inflorescence* terminal or sublateral, dichotomously branched several times, contracted or with long, divaricate primary branches, with dense, sessile or shortly (up to 1 mm) stalked in one and the same plant. *Calyx* 1.5–1.8 mm long, shortly hairy, lobes 5, spreading, narrowly linear-lanceolate to linear, acute, free to near base or at least for three quarters. *Corolla* white, c. 8 mm long, shortly hairy, tube narrowly cylindrical, limb short, salver-shaped, 1.8(–2) mm in diam., lobes triangular, acute. *Fruit* breaking up into two 2-celled pyrenes with a distinct keel at suture, only known in immature state, at that time ovoid, 2 mm long, 1.3 mm wide, green, white in mature state according to collector; stigma sessile, narrowly conical, c. 0.8 mm long, with a widened, deeply bilobed apex.

Distribution — *Malesia*: Moluccas, Buru, only known from type locality: SE of Bara (NW Buru).

Habitat — Riverine forests dominated by *Casuarina* at about 200–250 m altitude.

6. *Tournefortia sarmentosa* Lam.

Tournefortia sarmentosa Lam., *Tab. Encycl.* 1 (1791) 416; C.B. Rob., *Philipp. J. Sc., Bot.* 4 (1909) 694; I.M. Johnston, *J. Arnold Arbor.* 16 (1935) 147; 32 (1951) 115; Backer & Bakh. f., *Fl. Java* 2 (1965) 460. — Type: *Sonnerat* (P holo), Mauritius, cultivated.

Tournefortia tetrandra Blume, *Bijdr.* (1826) 845. — Type: unknown.

Tournefortia urvilleana Cham., *Linnaea* 4 (1829) 465; Miq., *Fl. Ind. Bat.* 2 (1858) 927. — Type: *Chamisso* (LE), Luzon.

Tournefortia hirsuta Reinw. ex Boerl., *Handl. Fl. Ned. Ind.* 2 (1899) 487, nomen, in syn.

Tournefortia horsfieldii Miq., *Fl. Ind. Bat.* 2 (1858) 927; C.B. Rob., *Philipp. J. Sc., Bot.* 4 (1909) 694. — Type: *Horsfield*, Java.

Tournefortia macrophylla K. Schum. & Lauterb., *Fl. Deutsch. Schutzgeb. Südsee* (1901) 520. — Type: *Lauterbach 2003* (B, destroyed), Papua New Guinea.

Tournefortia sarmentosa Lam. var. *magnifolia* Domin, *Bibl. Bot.* 89 (1928) 1097. — Type: *Dietrich 724*, Queensland.

Tournefortia glabrifolia Domin, *Bibl. Bot.* 89 (1928) 1098. — Type: *Domin*, Queensland.

Creeper or liana. Young branches dark brown, covered loosely by short, patent to subappressed hairs. *Leaves*: petiole 7–20 mm long; blade oblong-lanceolate to ovate lanceolate, 4–15 by 1.7–7 cm, margin entire, base rounded to truncate, apex acuminate, main nerves distinct especially below, upper side with a very few hairs, dense, minute whitish groups of mineralized cells usually present, lower side loosely appressed strigulose with irregularly directed hairs. *Inflorescence* dichotomously branched several times,

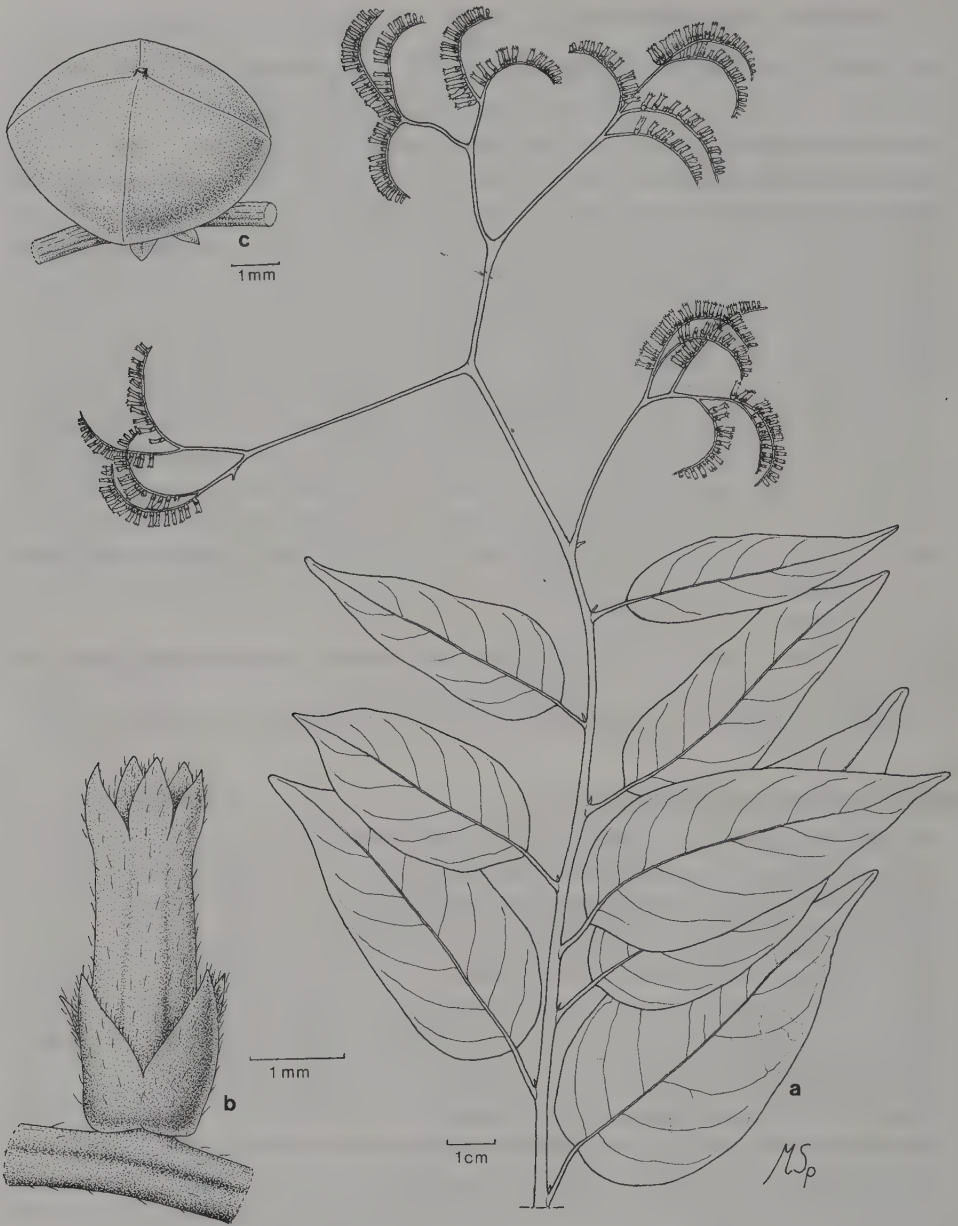


Fig. 13. *Tournefortia sarmentosa* Lam. a. Flowering branch; b. flower; c. fruit (Sulit & Conklin PNH 16900). Drawing M. Spitteler (a), J.H. van Os (b, c).

cymes dense when flowering, strongly accrescent and loose in fruit, terminal and axillary. *Flowers* numerous in 2 ranks, sessile. *Calyx* cup-shaped, 1.5–2 mm long, 3 mm wide, with appressed to patent short hairs on outer and inner side, lobes 5, free to base,

ovate-acuminate, 0.7–0.8 mm wide. *Corolla* salver-shaped, 6–9(–10) mm long, 4 mm in diam., densely strigulose outside, tube cylindrical, slightly narrower in lowest third, lobes plicate, ovate, acuminate, up to 2 mm long. *Stamens* inserted above middle of tube. *Fruit* depressed ovoid-subglobose, ribbed at border of pyrenes, rostrate, 2.5 mm long, 2.8 mm in diam. when dry, wall fleshy. — **Fig. 13.**

Distribution — Australia (N Queensland), Taiwan; *Malesia*: Sumatra, Malay Peninsula, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands (Lombok, Flores, Timor, Alor, Wetar), Moluccas, New Guinea.

Habitat — Dry areas, especially near sea; thickets (Backer & Bakhuizen f., l.c.).

7. *Tournefortia tetrandra* Blume

Tournefortia tetrandra Blume, Bijdr. (1826) 845; Steud., Nomencl. ed. 2, 2 (1841) 694 ('*tetragona*'); I.M. Johnston, J. Arnold Arbor. 16 (1935) 150; Backer & Bakh. f., Fl. Java 2 (1965) 460; Ng in Tree Fl. Malaya 4 (1989) 65. — Type: *Blume s.n.* (L. holo), Java.

Heliotropium scandens Noronha, Verh. Bat. Genootsch. 5 (1827) 78; Hassk., Cat. Hort. Bog. (1844) 137. — Type: not indicated.

Tournefortia tetrandra Blume var. *glabra* Hassk., Flora 25/2, (1842), Beibl. 27; Cat. Hort. Bog. (1844) 77; Pl. Jav. Rar. (1848) 492. — *Tournefortia glabra* (Hassk.) Zoll. & Mor. ex Zoll., Nat. Geneesk. Arch. Ned. Ind. 2 (1845) 5. — *Tetrandra glabra* (Hassk.) Miq., Fl. Ind. Bat. 2 (1858) 929. — Type: Hasskarl, Java.

Tournefortia wallichii DC., Prodr. 9 (1845) 527. — *Tetrandra wallichii* (DC.) Miq., Fl. Ind. Bat. 2 (1858) 928. — Type: Wallich 911, Singapore.

Tournefortia tetrandra Blume var. *angustifolia* Mor., Syst. Verz. (1845–46) 52, nomen nudum.

Tournefortia tetrandra Blume var. *longiflora* Hassk., Pl. Jav. Rar. (1848) 492. — Type: unknown.

Tetrandra zollingeri Miq., Fl. Ind. Bat. 2 (1858) 928. — Type: to be typified.

Creeper or liana. Branches smooth, greenish or reddish brown, with short, appressed hairs in herbaceous parts. *Leaves*: petiole 4–10 mm; blade ovate-lanceolate to lanceolate, 3–10 by 1–5 cm, margin entire to crenulate, base obliquely truncate, rarely subcordate, apex acute, nerves distinct on both sides, prominent and darker on pale lower surface when dry, short stiff hairs arising from tubercles of mineralized cells and such tubercles without hairs on upper, few stiff, short, appressed hairs mainly along nerves on lower side. *Inflorescence* branched, bearing cymes as branches of last order, terminal and/or lateral. *Flowers* subsessile, numerous in 2 ranks. *Calyx* narrowly cylindrical and tapering towards apex in flower, more explanate in fruit, 2.5 mm long, with few hairs mainly along margins, densely strigose on inner side, lobes 4, acuminate from a wider base, 0.7–0.8 mm wide. *Corolla* cylindrical, greenish to yellow, 9–10 mm long, 1–1.2 mm wide, lobes 4, erect, acute, folded along the middle. *Stamens* inserted at about the middle of the tube. *Fruit* depressed globose, with 2 beaks, 4 mm long and in diam., wall fleshy.

Distribution — Nicobar Islands, Sri Lanka; *Malesia*: Anambas and Natuna Islands, Sumatra, Malay Peninsula (according to Johnston 1935), Borneo, Java, Philippines, New Guinea.

Habitat — Mountain forests and scrubs.

Vernacular name — Ojot sisier (Sumatra).

TRICHODESMA

Trichodesma R.Br., Prodr. Fl. Nov. Holl. (1810) 496; Brand in Engl., Pflanzenr., fam. IV.252 (1921) 19. — Type species: *Borago zeylanica* Burm. f. [= *Trichodesma zeylanicum* (Burm. f.) R.Br.].

Annual or perennial herbs, sometimes suffrutescent. *Leaves* alternate or opposite, sessile or stalked. *Cymes* loose, often many-flowered, usually with bracts that may be similar to the upper stem leaves. *Flowers* pentamerous. *Calyx* on distinct, often fairly long pedicels, strongly accrescent in fruit, lobes free to the base or united in part. *Corolla* more or less rotate to funnel-shaped with a short tube and long-acuminate to cuspidate lobes, without scales in the throat. *Stamens*: anthers subsessile in the tube, oblong to linear, with long sterile awns that are twisted round each other. *Ovary* not divided in flower; style filiform, stigma small, globose. *Nutlets* 4, ovoid, triquetrous or nearly globose, smooth or rugose, sometimes hairy, with or without a distinct margin. — **Fig. 14, 15.**

Distribution — About 40 species in subtropical and tropical regions of Africa, Asia and Australia.

Uses — Both species from the Malesian region are used for medicinal purposes.

Notes — 1. Basic chromosome numbers are $x = 7, 11, 12$.

2. Brand (l.c.) divided the genus into 6 sections exclusively on characters of the fruits such as glabrous, bristly or hairy, marginate or immarginate, smooth or rugose. Both Malesian species belong to section *Leiocaryum* A.DC., which, including the type species *T. zeylanicum*, however, has to repeat the generic name *Trichodesma*. The section is characterized by smooth, shiny, immarginate nutlets.

KEY TO THE SPECIES

- 1a. All leaves sessile with a broad base. Calyx sagittate at base **1. *T. indicum***
- b. Lower leaves with a short stalk or at least tapering towards base. Calyx truncate at base **2. *T. zeylanicum***

1. *Trichodesma indicum* (L.) Sm.

Trichodesma indicum (L.) Sm. in Rees, Cyclop. 36/1 (1817) n. 1; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 696; Brand in Engl., Pflanzenr., fam. IV.252 (1921) 38. — *Borago indica* L., Sp. Pl. (1753) 137. — Type: *Herb. Linn.* 188/2 (LINN).

Annual herb. Stems 15–40 cm high, much branched, with spreading, not very dense hairs. *Leaves* sessile, oblong, lanceolate or lanceolate-oblong, lower leaves 5–8 by 0.8–2.2 cm, upper leaves 2–4.5 by 0.3–1.2 cm, base in lowermost leaves narrow, in the others broadly rounded, semiamplexicaulous, apex acute or obtusish, midrib distinct, sometimes also a few other nerves visible, hairs spreading-antrorse, arising from groups of mineralized cells on upper side, loose, crispulate on lower side. *Inflorescence* terminal on stem and branches, leafy, flowers axillary; pedicels 0.8–1.8 cm, curved downwards in fruit, with long, dense, spreading hairs. *Calyx* c. 1 cm long in flower, up to 1.3 cm in fruit, cleft to the base into narrowly triangular, basally sagittate lobes 1.2 mm

wide in flower, 2 mm wide in fruit, hairs loose, spreading from mineralized cells. *Corolla* funnel-shaped, lilac, tube c. 5 mm long, limb 1.3–1.5 cm in diam., lobes broadly rounded-acuminate, 7 mm long and wide. *Stamens*: anthers oblong, sterile, twisted apex 4–5 mm long, densely woolly. *Pistil*: style as long as calyx. *Nutlets* oblong ovoid, 5 mm long, 2–3 mm wide, smooth, whitish.

Distribution — Afghanistan, Pakistan, India, Burma (a separate variety), Mascarene Islands; *Malesia*: Philippines.

Habitat — Dry, sunny places, fields.

2. *Trichodesma zeylanicum* (Burm. f.) R.Br.

Trichodesma zeylanicum (Burm. f.) R.Br., Prodr. Fl. Nov. Holl. (1810) 496; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 696; Brand in Engl., Pflanzenr., fam. IV.252 (1921) 40; Backer & Bakh. f., Fl. Java 2 (1965) 462. — *Borago zeylanica* Burm. f., Fl. Ind. (1768) 41. — Type: Burman f., Fl. Indica t. 14, f. 2.

KEY TO THE VARIETIES

- 1a. Leaves oblong, oblong-lanceolate or broadly lanceolate, 0.8–4 cm wide **a. var. zeylanicum**
- b. Leaves linear to narrowly linear-lanceolate, sericeous, up to 0.5 cm wide **b. var. sericeum**

a. var. *zeylanicum*

Trichodesma zeylanicum (Burm. f.) R.Br. subsp. *eu-zeylanicum* Brand var. *vulgare* Brand f. *typicum* Brand & f. *longifolium* Brand in Engl., Pflanzenr., fam. IV.252 (1921) 41.

Annual, up to 1.75 m high. Stem much branched, angular, covered by spreading long hairs from groups of mineralized cells and very numerous short hairs. *Leaves* sessile, broadly lanceolate, lower leaves 6–12(–16) by 1–3(–5.5) cm, upper leaves 3–6 by 0.3–1.5 cm, base narrow, rounded, apex acute, midrib and several primary nerves strongly protruding on lower side, strigose to spreading bristly with hairs from groups of mineralized cells on upper, with few spreading, long bristles and denser, often antrorse, short hairs on lower side. *Cymes* scorpioid towards apex, rhachis with spreading long and appressed short hairs or only appressed hairs, basally leafy, leaves gradually decreasing in size, becoming bract-like towards apex; pedicels 0.8–3 cm long, with soft, appressed to spreading, flexuous hairs turning fuscous in plants from Madura. *Calyx* (1.2–)1.5–1.8 cm in flower, up to 2 cm in fruit, cleft to the base into long acute, 3(–4) mm long lobes, hairs appressed, silky, to spreading, usually white, turning fuscous in plants from Madura. *Corolla* funnel-shaped, bluish with 5 red dots, or violet, pink, or white, tube c. 8 mm long, limb 1.5–2(–2.5) cm in diam., lobes suborbicular or wider than long, 0.7–1 cm long, apiculate. *Stamens*: anthers shorter than awns, awns twisted, 0.8–1 cm long, with long hairs horizontally wound around anthers. *Pistil*: style 0.6–1.2 cm long, filiform. *Nutlets* ovoid, 5 mm long, c. 2 mm wide, smooth, shining, brown. — **Fig. 14, 15.**

Distribution — NE and E Africa, Comores, Madagascar, Mascarene Islands, India, Sri Lanka; *Malesia*: Java (Madura), Philippines, Lesser Sunda Islands (Flores, Sumba, Timor, Alor), New Guinea.



Fig. 14. *Trichodesma zeylanicum* (Burm. f.) R. Br. a. Flowering plant; b. flower; c. fruit in calyx (Turner s. n.). Drawing M. Spitteler.

Fig. 15. *Trichodesma zeylanicum* (Burm. f.) R. Br. Top of flowering stem. Flores. Photo L. van der Pijl.



b. var. sericeum (Lindl.) Benth.

Trichodesma zeylanicum (Burm. f.) R. Br. var. *sericeum* (Lindl.) Benth., Fl. Austral. 4 (1869) 405. — *Trichodesma sericeum* Lindl. in Mitch., J. Trop. Austral. (1848) 258. — *Trichodesma zeylanicum* subsp. *eu-zeylanicum* Brand var. *australe* Brand f. *sericeum* (Lindl.) Brand in Engl., Pflanzenr., fam. IV. 252 (1921) 42. — Type: Mitchell, Australia, Belyando River.

Leaves 3–6.5 by 0.2–0.3 cm, with revolute margins. Indument in all parts silky, hairs partly from groups of mineralized cells, but covering them completely, very dense, of nearly equal length, appressed antrorse. Calyx usually 1.2–1.3 cm long.

Distribution — Australia; *Malesia*: Lesser Sunda Islands (Flores, Sumba, Timor).

TRIGONOTIS

Trigonotis Steven, Bull. Soc. Nat. Moscou 24, 1 (1851) 603; I.M. Johnston, J. Arnold Arbor. 21 (1940) 57; 33 (1952) 68; P. Royen, Pac. Sc. 29 (1975) 81. — Type species: *Trigonotis clavata* Steven [= *Trigonotis pedunculare* (Trev.) Benth.].

Zoelleria Warb., Bot. Jahrb. 16 (1893) 28. — Type species: *Zoelleria procumbens* Warb. [= *Trigonotis procumbens* (Warb.) I.M. Johnston].

Havilandia Stapf, Trans. Linn. Soc. Lond. II, Bot. 4 (1894) 209; I.M. Johnston, J. Arnold Arbor. 16 (1935) 190. — Type species: *Havilandia borneensis* Stapf [= *Trigonotis borneensis* (Stapf) I.M. Johnston].

Creeping, decumbent or ascending herbs with simple or branched stems, sometimes forming large mats or cushions. *Leaves* either in basal rosettes or cauline, alternate, stalked or not, in creeping species sometimes all in one plane by twisting of the petioles. *Flowers* solitary, axillary or extra-axillary, or in elongated, terminal or lateral, scorpioid cymes without leaves or bracts, or with the lowermost flowers in the axils of leaf-like bracts. *Calyx* with 5 lobes imbricate in bud. *Corolla* lobes 5 or 6, invaginate at base, forming hollow appendages bulging into the throat. *Stamens* isomerous with corolla, filaments very short, inserted in the tube of corolla, anthers opening introrsely with two longitudinal slits. *Ovary* composed of 4 or (7-)8-10 carpels on a cup-shaped receptacle, style short, stigma bilobed. *Nutlets* 4 or (7-)8-10, either with a sharp angle dorsally, dorso-ventrally compressed, or rounded dorsally, slightly compressed laterally, ribs sometimes with a narrow wing, smooth or finely papillate to tuberculate, glabrous or with hairs along the margins, shiny or dull. — **Fig. 16, 17.**

Distribution — About 50 species in Central Asia, China, Japan to *Malesia*: Borneo, Philippines, and New Guinea.

Habitat — Most of the species grow at higher altitudes, mainly in the montane and subalpine zone, a few also lower down or in the alpine zone.

Notes — 1. In the few species counted polyploidy is prevalent with the diploid numbers $2n = 36$ or 48 .

2. *Trigonotis* was usually regarded as a member of *Lithospermeae*, but Riedl (1968) made it the type genus of a separate tribe *Trigonotideae*, in which it is the sole member of subtribe *Trigonotidinae*. *Trigonotideae* include all those genera which are nearest to the root of the other tribes within *Boraginoideae*. Its closest relatives outside *Trigonotideae* seem to be *Trigonocaryum* and *Myosotis*. As in the latter, in some of its species nutlets are pyramidal with the areola shortly stipitate.

3. *Zoelleria* Warb. has been regarded as the type of a separate, monotypic tribe *Zoellerieae* by Gürke (1897) for the aberrant number of carpels (7-10), but agrees in all other characters with what Stapf described as a new genus *Havilandia*. *Havilandia* was characterized by dorsally rounded, laterally compressed nutlets, while in typical *Trigonotis* they are dorsally angulate and compressed dorso-ventrally. Along with this difference went the growth habit: creeping with solitary, axillary flowers in *Havilandia*, apically erect with naked or nearly naked cymes in *Trigonotis* s.str. With the discovery of *Trigonotis abata* I.M. Johnston, this correlation did not hold any longer: it combined the growth habit of *Havilandia* with the shape of the nutlets of *Trigonotis*. For this reason, Johnston united all three genera in 1940. *Trigonotis minuta* seems to keep a similar intermediate position according to Van Royen's description of the nutlets. The present treatment closely follows the two excellent papers of Johnston (1940) and Van Royen (1975).

References: Gürke, M., Boraginaceae, in Engl. & Prantl, Nat. Pflanzenfam. 4, 3a (1897) 71-131; Stapf, O., Trans. Linn. Soc. Lond. II, Bot. 4 (1894) 209; Johnston, I.M., J. Arnold Arbor. 21 (1940) 59; Riedl, H., Österr. Bot. Z. 115 (1968) 291; Van Royen, P., Pac. Sc. 29 (1975) 81; Alpine Fl. New Guinea 4 (1983) 3094.

KEY TO THE SPECIES

- 1a. Ovary 7–10-lobed, nutlets 7–10 2
- b. Ovary 4-lobed; nutlets 4 3
- 2a. Corolla 7–9 mm in diam. Leaves elliptic- to obovate-oblong, strigose on margin and midrib, otherwise glabrous **13. *T. pleiomera***
- b. Corolla c. 4 mm in diam. Leaves orbicular to ovate, conspicuously strigose on both faces **14. *T. procumbens***
- 3a. Leaves linear to linear-lanceolate, acute, not longer than 9 mm ... **9. *T. minuta***
- b. Leaves wider, oblong-obovate to oblanceolate, if linear then much longer than 9 mm 4
- 4a. Nutlets angulate dorsally, dorso-ventrally compressed; plants prostrate, flowers solitary above axils of upper leaves **1. *T. abata***
- b. Nutlets either angulate dorsally, dorso-ventrally compressed and plants upright in upper part with elongated cymes or nutlets rounded dorsally, or plants prostrate with solitary flowers in axils of upper leaves 5
- 5a. Nutlets angulate dorsally, dorso-ventrally compressed; plants upright in the upper part, with elongated cymes 6
- b. Nutlets rounded dorsally, laterally slightly compressed; plants creeping, prostrate; flowers solitary in the axils of upper leaves 12
- 6a. Bases of lower leaves decurrent, upper leaves stalked 7
- b. Bases of lower leaves rounded or tapering into a petiole 8
- 7a. Leaves strigose along margins only; cymes axillary with 4–6 flowers; stems glabrous **17. *T. vestita***
- b. Stems and leaves hirsute on whole surface; cymes terminal, often bifurcate, with more numerous flowers **7. *T. hirsuta***
- 8a. Ovary and fruit finely hairy; leaves linear to oblong or oblong-lanceolate **6. *T. haackii***
- b. Ovary and fruit glabrous; leaves oblong to elliptic 9
- 9a. Calyx united for half of its length, lobes ovate-triangular **2. *T. apoense***
- b. Calyx united for less than half of its length, lobes narrowly ovate to ovate-lanceolate 10
- 10a. Stem densely patent hairy in its lower part, hairs reddish brown when dry. Leaves of flowering stems 0–1, broadest near base, semiamplexicaulous **16. *T. subrosulata***
- b. Stem with more or less appressed, antrorse hairs in its whole length, hairs permanently white. All leaves tapering towards base, stalked 11
- 11a. Corolla 4 mm long, tube c. 2 mm; both leaf surfaces densely strigose **12. *T. philippinensis***
- b. Corolla 3–9 mm long, tube 2–3(–5) mm; upper leaf surface laxly strigose, hairs sometimes in irregular patches **8. *T. inoblita***
- 12a. Nutlets ciliolate along their margins **4. *T. ciliolata***
- b. Nutlets glabrous or minutely papillate 13

- 13a. Plant pulvinate with short stems crowded densely together. Leaves not longer than 8 mm **5. *T. culminicola***
 b. Plant not pulvinate, with elongate, more or less creeping stems. Leaves distinctly longer 14
 14a. Nutlets minutely papillate, gray or light-brown, dull 15
 b. Nutlets smooth, blackish or black, rarely ivory white, shiny 16
 15a. Pedicels 0.5–1 mm long. Corolla 3–3.5 mm long, 4.5 mm across **10. *T. opaca***
 b. Pedicels 8–12 mm long in flower, up to 18 mm in fruit. Corolla 9 mm long, 12 mm across **15. *T. robusta***
 16a. Leaves oblanceolate, gradually contracted into the petiole; nutlets lanceolate. Pedicels 2–5 mm long **3. *T. borneensis***
 b. Leaves obovate to elliptic, abruptly contracted into a short, sheathing petiole; nutlets short. Pedicels 1–3 mm in flower, up to 7 mm in fruit **11. *T. papuana***

1. *Trigonotis abata* I.M. Johnston

Trigonotis abata I.M. Johnston, J. Arnold Arbor. 21 (1940) 58; Van Royen, Pac. Sc. 29 (1975) 88; Alpine Fl. New Guinea 4 (1983) 3106. — Type: *Brass & Meijer Drees 9838* (A), Irian Jaya, Mt Trikora (Wilhelmina).

Creeping herbs, rooting at nodes. Stems up to 30 cm long, antrorse strigose, finally glabrescent. *Leaves* ovate or elliptic, (0.4–)0.8–2.2 by (0.2–)0.4–1 cm, sometimes slightly asymmetric, base rounded, abruptly tapering into the 1–2 mm long, sheathing, often twisted petiole or sessile, lateral nerves 1 or 2 on either side of midrib, leaves antrorse strigose on both side, more patent on upper side, denser on midrib below. *Flowers* solitary, extra-axillary; pedicels 3–4 mm long in flower, 7–12 mm in fruit, antrorse strigose. *Calyx* 1.5–2.5 mm in flower, up to 3 mm in fruit, antrorse hairy on the whole surface or along midrib of lobes only, lobes ovate-lanceolate to ovate, c. 1.5 mm long, 1 mm wide, acute to acuminate, with a black, linear gland outside below tip. *Corolla* white with yellow throat, 4–5 mm across, lobes obovate; fornicies kidney-shaped, finely ciliate. *Stamens* c. 1 mm long, anthers 0.5 mm. *Pistil*: style c. 1 mm long. *Nutlets* 4, pyramidal, dorsally convex, ventrally with a sharp angle, 2–3 mm long, 1–1.5 mm wide, brownish black, with 3 narrow, acute crests.

Distribution — *Malesia*: mountains of New Guinea, endemic.

Habitat — In damp places on landslides, open, sandy beds of streams, in moss cushions of subalpine shrubberies, 1670–3650 m altitude.

Note — Some specimens with very small, nearly sessile leaves usually not longer than 4–6 mm and densely crowded, shorter stems forming mats like *T. culminicola* seem to belong to this species, but may represent a separate variety or subspecies. Further investigations in this matter are necessary.

2. *Trigonotis apoensis* Elmer

Trigonotis apoensis Elmer, Leaf. Philipp. Bot. 7 (1915) 2562. — Type: *Elmer 11500* (not seen), Mindanao.

Creeping, biennial herbs with prostrate, rooting, branched stems, lateral branches or tufts of leaves arising from bracts at the nodes. Stems slightly succulent, glabrous or subglabrous, with erect ends. *Leaves* alternate along runners, tufted distally, narrowly elliptic to broadly oblong, petiole 2–8 cm long, sheathing the stem, greyish strigose, lamina up to 6 by 3 cm, but usually much smaller, rounded at base, apex rounded-apiculate, with 3–5 lateral nerves on either side paler below, with appressed, white hairs on both sides, denser along the midrib below. *Cymes* arising from the uppermost leaf axils, with a distinct peduncle, leafy bracteate, flowers crowded towards scorpioid top; bracts elliptic, acute, 5 mm long, 2.5 mm wide; pedicels 3–4 mm long, minutely strigose. *Calyx* 4 mm long and wide, divided to the middle into 5 ovate-triangular, slightly unequal teeth overlapping towards base, sparsely strigose. *Corolla* 3.5 mm long, tube about as long as limb, lobes elliptic to shortly obovate, 1.5 mm long; fornicies short and broad. *Stamens*: filaments less than 0.5 mm, anthers 0.75 mm. *Pistil*: style 1–1.5 mm long, stigma minute. *Nutlets* pyramidal, dark brown, not seen at maturity.

Distribution — *Malesia*: Philippines (Mindanao).

Habitat — Fertile, moist humus at banks of creeks.

Vernacular name — Salimbangande.

Note — The description is taken from Elmer's diagnosis of the species, that does not seem to have been collected in more recent times.

3. *Trigonotis borneensis* (Stapf) I.M. Johnston

Trigonotis borneensis (Stapf) I.M. Johnston, J. Arnold Arbor. 21 (1940) 63; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 94. — *Havilandia borneensis* Stapf, Trans. Linn. Soc. Lond. II, 4 (1894) 209, t. 16. — *Lithospermum borneense* (Stapf) Boerl., Handl. Fl. Ned. Ind. 2 (1899) 488. — *Plagiobothrys borneensis* (Stapf) I.M. Johnston, Contr. Gray Herb. 73 (1924) 78. — Type: *Haviland 1059* (K holo), Sabah, Mt Kinabalu.

Stems long prostrate or creeping, sometimes rooting, in their lower parts naked, in their distal part with a few dichotomous branches, with distichous leaves, appressed greyish strigillose. *Leaves* sessile, semi-amplexicaulous and nearly sheathing the stem, 1.5–2.5 by 0.4–0.7 cm, slightly emarginate at apex, in apical part appressed, towards base spreading ciliate at margin, on upper side appressed strigillose near apex, on lower side glabrous except along midrib, without lateral veins. *Flowers* single in the axils of leaves; pedicel 2–5 mm long, appressed strigillose. *Calyx* at last 6–7 mm long, cleft for two thirds, lobes bristly-ciliate, spreading in fruit. *Corolla* funnel-shaped, 3.5–4 mm long, lobes as long as tube, obovate. *Stamens*: anthers subsessile, c. 0.5 mm long. *Pistil*: style c. 1 mm long. *Nutlets* c. 2 mm long, pyramidal, substipitate, sharply angled ventrally.

Distribution — *Malesia*: Borneo, only known from Mt Kinabalu area.

Habitat — Marshy places.

4. *Trigonotis ciliolata* I.M. Johnston

Trigonotis ciliolata I.M. Johnston, J. Arnold Arbor. 33 (1952) 68; Van Royen, Pac. Sc. 29 (1975) 88; Alpine Fl. New Guinea 4 (1983) 3108. — Type: *Kanehira & Hatusima 13883*, Irian Jaya, Arfak Mts.

Small creeping herbs. Stems densely patently strigose. *Leaves* shortly petiolate, petiole 2–6 mm long, blade ovate, 1.6–2.6 by 0.8–2.2 cm, base rounded, abruptly tapering into the petiole, acute to apiculate at apex, subappressed strigose, densest along midrib on lower side. *Flowers* solitary, extra-axillary; pedicels antrorse strigose, 12–15 mm long. *Calyx* 3.5–5 mm long, antrorse strigose on outer and to a lesser degree on inner side, lobes lanceolate, 3–3.5 by 1–1.5 mm, acute, elongated to 4.5 mm in fruit. *Corolla* white, glabrous, 5–7 mm long, tube 2.2–2.5 mm, lobes orbicular, 3–4 mm in diam., fornices kidney-shaped, 1 mm broad, finely hairy. *Stamens* 1.2 mm long, anthers 0.7 mm. *Pistil*: style 1–1.3 mm long. *Nutlets* pyramidal, c. 1 mm long, dorsal side convex, the other surfaces flat, 2 mm wide, margins acute, ciliate, black, smooth.

Distribution — *Malesia*: endemic in western New Guinea.

Habitat — Probably wet, open grasslands, about 1900 m altitude.

5. *Trigonotis culminicola* P. Royen

Trigonotis culminicola P. Royen, Pac. Sc. 29 (1975) 90; Alpine Fl. New Guinea 4 (1983) 3112. — Type: Hoogland & Pullen 5790 (L. holo), Papua New Guinea, Mt Wilhelm.

Small, creeping herbs forming dense cushions or mats. Stems short, numerous, densely antrorse strigose. *Leaves* obovate, spatulate or oblong, 5–8 by 0.3–0.4 mm, base gradually tapering into the 1–3 mm long, sheath-like petiole, apex rounded, retuse or mucronulate, without lateral veins, sparsely antrorse strigose above, glabrous below except midrib and margins. *Flowers* solitary, extra-axillary; pedicels spreading strigose, 2–3.5 mm long in flower, up to 4.5 mm in fruit. *Calyx* 2.5–3.5 mm long in flower, coherent base 0.5–1 mm in flower, accrescent to 1.5–2 mm in fruit, lobes 1–1.5 mm wide, not accrescent, acutish or obtuse, apiculate, with a black gland at tip, white antrorse strigose on outside along midrib and margins. *Corolla* white or pink or lavender, throat yellow, glabrous, tube 1.5–2.5 mm long, lobes orbicular, 1.5 mm in diam., rounded or retuse; fornices kidney-shaped, ciliate. *Stamens* c. 1 mm long, anthers oblong-ovoid, c. 0.7 mm long. *Pistil*: style c. 0.5 mm. *Nutlets* pyriform, dorsally rounded, c. 1.2 mm long, black, smooth.

Distribution — *Malesia*: mountains of New Guinea, endemic.

Habitat — Moist ground among gravel and in rock crevices, 3150–4480 m altitude.

6. *Trigonotis haackii* F. Muell.

Trigonotis haackii F. Muell., Trans. Roy. Soc. Vict., N. S. I/2 (1889) 30; Van Royen, Pac. Sc. 29 (1975) 83; Alpine Fl. New Guinea 4 (1983) 3097. — Type: MacGregor s.n. (MEL holo), Papua New Guinea, Mt Victoria.

Erect or decumbent herbs. Stems up to 35 cm high, covered with appressed, white hairs. *Leaves* nearly opposite to alternate, linear-spatulate to elongate-spatulate, 1.8–4 by 0.2–0.4 cm, tapering towards base into a very short petiole, acute at apex, without distinct lateral veins, sparsely appressed white strigose above, subglabrous with more hairs only along midrib below. *Cymes* up to 5 cm long, ebracteate; pedicels 2.5–4 mm

long, strigose. *Calyx* 3.5–5 mm long, divided to near base into ovate to ovate-elliptic, acute lobes with black glands at the very tip, strigose outside mainly along midrib and margins, glabrous inside. *Corolla* glabrous, tube 2.5–3 mm long, lobes orbicular to broadly ovate, 2–2.5 mm in diam.; fornicies bilobed, finely papillate. *Stamens*: filaments short, anthers c. 1 mm long, oblong. *Pistil*: style 1–1.5 mm long, stigma slightly bilobed. *Nutlets* obliquely pyriform, c. 1 mm long, rounded dorsally, with a sharp angle ventrally, dull brown, with few fine hairs.

Distribution — *Malesia*: New Guinea, endemic.

Habitat — Open, wet grasslands.

7. *Trigonotis hirsuta* Steenis

Trigonotis hirsuta Steenis, Bot. Jahrb. 86 (1967) 398. — Type: *van Steenis* 6202 (L holo; BO), N Sumatra.

Prostrate herb. Stems densely covered with long, patent, rigid hairs. *Leaves* oblong to broadly spatulate, petiole 1–2 cm long, blade 3–5 by 1.5–2 cm, decurrent at base, apex rounded, scarcely acute, sometimes mucronulate, with patent, rigid hairs on white tubercles on lower side and on upper side along veins. *Cymes* often forked, ebracteate; pedicels 1–1.5 mm long, patent hirsute. *Calyx* hirsute as other parts, c. 1.5 mm long, divided to base into spatulate-oblong, obtuse or acutish lobes. *Corolla* glabrous, tube as long as calyx, lobes rounded, suborbicular, 1.5 mm in diam. *Stamens*: anthers oblong, on very short filaments. *Pistil*: style c. 1 mm long, stigma minute, capitate. *Nutlets* tetrahedral, 1 mm long, with 3 distinctly costate angles, brown, smooth, shiny, glabrous.

Distribution — *Malesia*: N Sumatra, endemic.

Habitat — Found, for instance, in elephant trails together with *Urticaceae* and *Amaranthaceae*, at 1300–2000 m altitude.

8. *Trigonotis inoblita* F. Muell.

Trigonotis inoblita F. Muell., Trans. Roy. Soc. Vict., N.S. I/2 (1889) 31; Van Royen, Pac. Sc. 29 (1975) 83; Alpine Fl. New Guinea 4 (1983) 3097. — Type: *MacGregor s.n.* (MEL), Papua New Guinea, Owen Stanley Range.

Decumbent or more commonly erect herbs. Stems up to 40 cm high, simple or branched, leafy mainly in the upper half, densely, often antrorse appressed strigose. *Leaves* broadly or narrowly elliptic, spatulate, obovate, oblong, elliptic- or obovate-oblong to oblong-ovate, petiole 0.5–3.5 cm long, glabrous above, strigose below, blade 2–12 by 0.7–3 cm, tapering into a petiole at base, obtuse or rounded and apiculate or acuminate at apex, with 5–7 lateral nerves on either side of midrib, sparsely strigose above, strigose below and along margins, denser along midrib. *Cymes* terminal or axillary, simple or branched, with 10–40 flowers, ebracteate, rhachis densely strigose; pedicels 1–7 mm long, densely strigose. *Calyx* 1.5–4 mm long, cleft to the base into 5 ovate to ovate-lanceolate, oblong or oblong-elliptic lobes 0.5–1 mm wide, with acute tips and a black gland just below tip, appressed strigose outside, sometimes only along ribs, glabrous

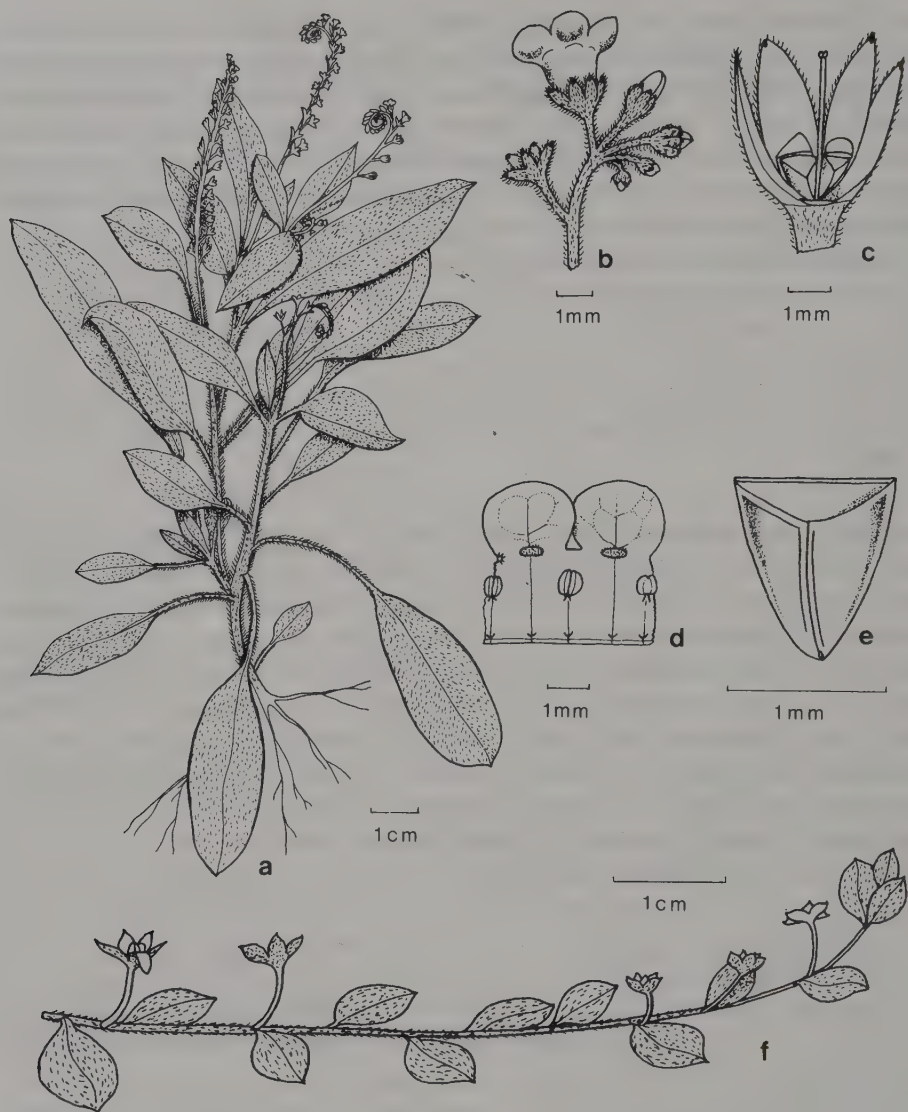


Fig. 16. *Trigonotis inoblita* F. Muell. var. *inoblita*. a. Flowering plant; b. top of inflorescence; c. calyx with fruits; d. part of corolla with stamens; e. fruit (a, e: Hoogland & Schodde 6911; b–d: Brass 31358). — *T. procumbens* (Warb.) I.M. Johnston. f. Apical part of plant (Hellwig 331). Drawing P. van Royen. Reproduced from Van Royen, Alpine Flora New Guinea 4.

inside. *Corolla* white or lobes pale purple at apex, throat pale yellow, 3–9 mm long, 5–12 mm in diam., tube 2–3(–5) mm long, lobes suborbicular to orbicular, 1.5–5 mm wide; fornicies kidney-shaped, c. 1 mm wide, finely ciliate. *Stamens*: filaments very short, anthers c. 0.7 mm long. *Pistil*: style slightly shorter than calyx, stigma bilobed. *Nutlets* pyramidal, 1–1.5 mm long, dark brown, smooth, with ribbed angles. — **Fig. 16 a–e.**

Distribution — *Malesia*: throughout New Guinea, endemic.

Habitat — Damp, shady places, along rivulets, in alpine grassland, under boulders, in mossy slopes, under trees.

KEY TO THE VARIETIES

- 1a. Flowers 3–3.5 mm long, 3 mm across. Pedicels 1–4 mm long . . . **a. var. *inoblita***
b. Flowers 4–8 mm long, 5–12 mm across. Pedicels 3–7 mm long
..... **b. var. *archboldii***

a. var. *inoblita*

P. Royen, Pac. Sc. 29 (1975) 84; Alpine Fl. New Guinea 4 (1983) 3101.

Distribution — Whole area of the species.

b. var. *archboldii* (I.M. Johnston) P. Royen

Trigonotis inoblita F. Muell. var. *archboldii* (I.M. Johnston) P. Royen, Pac. Sc. 29 (1975) 88; Alpine Fl. New Guinea 4 (1983) 3102. — *Trigonotis archboldii* I.M. Johnston, J. Arnold Arbor. 21 (1940) 58. — Type: *Brass & Meijer Drees 9838* (A holo), Irian Jaya, Mt Trikora (Wilhelmina).

Distribution — *Malesia*: New Guinea.

9. *Trigonotis minuta* (Wernham) I.M. Johnston

Trigonotis minuta (Wernham) I.M Johnston, Contr. Gray Herb. 81 (1928) 81; Van Royen, Pac. Sc. 29 (1975) 87; Alpine Fl. New Guinea 4 (1983) 3103. — *Lithospermum minutus* Wernham, Trans. Linn. Soc. Lond. II, 9 (1916) 118. — Type: *Boden Kloss (Wollaston Exp.)*, Irian Jaya, Mt Jaya (Carstenz).

Small, erect herb. Stem 4 cm high. *Leaves* densely arranged along whole length of stem, linear, sessile with broad base, clasping stem, 6–9 by 0.1–0.2 mm, acute, only midrib distinct, ciliate along margin and midrib below, with longer hairs towards base. *Flowers* solitary, terminal. *Calyx* 2–3 mm long, cleft to the base, lobes lanceolate, acuminate, 1–1.5 mm wide, ciliate along midrib and margin. *Corolla* glabrous, tube 1.5–2 mm long, lobes orbicular, c. 2.5 mm wide; fornicies kidney-shaped, papillate. *Stamens* 0.5–0.8 mm long, anthers ovoid, 0.5 mm. *Nutlets* pyramidal, 1 mm long, 0.7 mm wide, with sharp angles, blackish, smooth, shiny.

Distribution — *Malesia*: New Guinea, only known from the type collection.

Habitat — Open moraines and alpine grasslands, 3140–4400 m altitude.

10. *Trigonotis opaca* (I.M. Johnston) I.M. Johnston

Trigonotis opaca (I.M. Johnston) I.M. Johnston, J. Arnold Arbor. 21 (1940) 62; Van Royen, Pac. Sc. 29 (1975) 92; Alpine Fl. New Guinea 4 (1983) 3116. — *Havilandia opaca* I.M. Johnston, J. Arnold Arbor. 16 (1935) 190. — Type: *Brass 4178* (A holo), Papua New Guinea, Wharton Range.

Small, creeping herbs forming large, more or less dense mats. Stems much branched, densely appressed, white, antrorse strigose. *Leaves* oblong to oblong-ovate, petiole 1–2 mm long, blade 4–7 by 0.2–0.4 mm, base cuneate, abruptly narrowed into the petiole, apex rounded or retuse, with 3 or 4 lateral veins on either side of midrib, glabrous except lower side of petiole, margins and midrib on lower side, which are densely strigose. *Flowers* solitary in leaf axils; pedicels 0.5–1 mm long, antrorse strigose. *Calyx* 3–3.5 mm long, lobes ovate-elliptic, 1.7–2.5 by 1 mm, acute, strigose along margins and midrib. *Corolla* white, as long as calyx, up to 4.5 mm in diam., tube 1.5–2 mm, lobes rounded obovate, 1.2–1.5 mm wide, finely papillate inside; fornicies trapeziform, yellow, c. 0.5 mm wide, finely papillate. *Stamens* c. 0.7 mm, anthers 0.4–0.6 mm long. *Pistil*: style c. 0.7 mm long. *Nutlets* 4, ovoid, 1 mm long, 0.5 mm wide, dorsally rounded, with a ventral crest and sharp, lateral angles, light brown to grey, dull, minutely papillate.

Distribution — *Malesia*: Papua New Guinea, endemic.

Habitat — Open, wet grasslands on black, peaty soils, once found on dead tree-fern, 2660–2950 m altitude.

11. *Trigonotis papuana* (Hemsl.) I. M. Johnston

Trigonotis papuana (Hemsl.) I. M. Johnston, J. Arnold Arbor. 21 (1940) 63; P. Royen, Pac. Sc. 29 (1975) 93; Alpine Fl. New Guinea 4 (1983) 3118. — *Havilandia papuana* Hemsl., Kew Bull. (1899) 107. — Syntypes: *Giulianetti s. n.*, *English s. n.* (K), Papua New Guinea.



Fig. 17. *Trigonotis papuana* (Hemsl.) I. M. Johnston. Flowering plant. Naitmambi Range, Papua New Guinea. Photo P. van Royen, 1976.

Creeping herbs, often forming large mats. Stems much branched, appressed antrorse strigose. *Leaves* in two rows flat on the ground by twisting of the sheath-like, clasping petiole, petiole 1–7 mm long, blade oblong, oblong-ovate or spatulate, 0.4–2 by 0.2–0.9 cm, abruptly narrowed into petiole, apex rounded or often retuse, glabrous above, strigose along midrib alone below, margins antrorse strigose. *Flowers* solitary, axillary or extra-axillary; pedicels 1–3 mm long in flower, up to 7 mm in fruit, antrorse strigose. *Calyx* 3.5–4.5 cm long, divided to about 1–1.5 mm above base into ovate to lanceolate, 1–1.5 mm wide, acutish lobes with black gland outside below apex, antrorse strigose outside along midrib and margins. *Corolla* white or pink, purple or white with bluish tinge, tube 1–1.5 mm long, lobes ovate-orbicular or sometimes spatulate, 1.5–3 by 1.5–2.5 mm, rounded, finely papillate inside; fornices yellow, kidney-shaped, c. 0.5 mm wide, 0.2 mm long, finely ciliate. *Stamens* 1 mm long, anthers 0.8 mm. *Pistil*: style 0.7–1 mm long. *Nutlets* obpyriform, 1–1.5 mm long, c. 1 mm wide, acute, dorsally rounded, with a narrow crest ventrally, dark brown, rarely ivory white, smooth, glabrous. — **Fig. 17.**

Distribution — *Malesia*: New Guinea, widespread, endemic.

Habitat — Wet, open places in grasslands, swamps, seepage slopes, along rivulets, wet landslides, 2900–4100 m altitude.

Vernacular name — Kua'pepo (Mendi).

Note — Obviously the most common species on New Guinea.

12. *Trigonotis philippinensis* Merr.

Trigonotis philippinensis Merr., Philipp. J. Sc. 1, Suppl. (1906) 228; C.B. Rob., Philipp. J. Sc., Bot. 4 (1909) 697. — Type: *Merrill 4700*, Luzon.

Erect or slightly prostrate. Stems up to 25 cm high, with few branches, more or less hispid pubescent. *Leaves* oblong, elliptical, oblong-obovate or subspathulate, tapering into a distinct, slender, 0.4–2.5 cm long petiole, blade 0.8–3 by 0.6–1.3 cm, apex acute or rounded to retuse, distinctly apiculate, lateral veins indistinct, antrorse white strigose on upper as well as midrib and margins on lower side, with few scattered hairs on lower surface. *Cymes* lateral, solitary, ebracteate, with distinct peduncle, rhachis antrorsely strigose; pedicels antrorse strigose, less than 1 mm long in flower, elongated to 3 mm, in the lowermost flowers to 5–6 mm in fruit. *Calyx* 1.5–2 mm long in flower, up to 3 mm long in fruit, strigose, lobes narrowly ovate, acute, c. 2 mm long at last. *Corolla* white, 4 mm long, tube nearly 2 mm long, lobes obovate to suborbicular, broadly rounded, c. 2 mm wide; fornices fairly broad. *Stamens*: filaments very short, anthers oblong, c. 0.8 mm long. *Pistil*: style c. 1 mm long. *Nutlets* tetrahedral with 4 sharp angles, c. 1 mm long, black, shiny, glabrous.

Distribution — *Malesia*: Philippines (N Luzon), endemic.

Habitat — Damp, mossy cliffs just below limit of mossy forest at about 1900 m altitude.

Note — Specimens from the classical localities do not quite agree with Merrill's diagnosis. The most important difference are the cymes arising from the axils of some of the

lowermost, long since withered leaves and not terminal as Merrill says. The calyx is 3 mm long only at the very last stage of fruiting. Nevertheless, there can be little doubt about their identity.

13. *Trigonotis pleiomera* I.M. Johnston

Trigonotis pleiomera I.M. Johnston, J. Arnold Arbor. 21 (1940) 61; Van Royen, Pac. Sc. 29 (1975) 94; Alpine Fl. New Guinea 4 (1983) 3120. — *Clemens* 5989 (A holo), Papua New Guinea, Mt Sarawaket.

Creeping, much branched herbs growing solitary or in dense mats. Stems up to 35 cm long, appressed strigose. *Leaves* usually seemingly distichous due to twisted petioles, petioles 1–3 mm long, blade elliptic, obovate, oblong or elliptic- to obovate-oblong, 0.8–2 by 0.3–1 cm, tapering towards base, tips rounded or obtuse, apiculate, lateral nerves 3 or 4 on each side of midrib, sparsely appressed antrorse strigose along margins and on midrib below. *Flowers* solitary, extra-axillary; pedicels appressed antrorse strigose, 8–15 mm long. *Calyx* 3–5 mm long, divided to near base into ovate or oblong-ovate, 2–2.5 mm wide, acute lobes, antrorse strigose along margins and midribs. *Corolla* white, purplish, pink or pale purple blue, 7–9 mm diam., tube 3–4 mm long, lobes 5 or 6, glabrous, orbicular-ovate, rounded, 4–5 by 3.5–4.5 mm; fornicies kidney-shaped, c. 0.5 mm wide, finely hairy. *Stamens* 1–1.5 mm long, anthers oblong-ovoid, 1 mm long. *Pistil*: style 1–1.5 mm long. *Nutlets* 7–10, obliquely ovoid, 1–1.5 mm long, 0.5–1 mm wide, acute, dorsally convex, with sharp crest, light grey, shiny, smooth.

Distribution — *Malesia*: New Guinea, endemic.

Habitat — Slightly shaded, wet parts of grasslands, open places in montane forests, 2130–4100 m altitude.

14. *Trigonotis procumbens* (Warb.) I.M. Johnston

Trigonotis procumbens (Warb.) I.M. Johnston, J. Arnold Arbor. 21 (1940) 62; Van Royen, Pac. Sc. 29 (1975) 89; Alpine Fl. New Guinea 4 (1983) 3109. — *Zoelleria procumbens* Warb., Bot. Jahrb. 17 (1893) 28. — Type: *Hellwig* 331 (B holo, destroyed), Papua New Guinea, Finisterre Mts.

Creeping herbs, sometimes growing in clumps. Stems long, slender, much branched with suberect distal part, green or purple, antrorse strigose. *Leaves* ovate, elliptic or intermediate, sometimes suborbicular, petiole 1–12 mm long, densely or sparsely strigose, blade 0.3–4.5 by 0.2–3 cm, base cuneate, abruptly contracted to petiole, apex rounded or obtuse and apiculate, with 3 or 4 lateral nerves on each side of midrib, appressed antrorse strigose on both sides, often denser along midrib below. *Flowers* solitary, axillary; pedicels 3–8 mm long, appressed antrorse strigose. *Calyx* appressed strigose outside and inside, basal tube 0.5–1 mm long in flower, up to 2 mm in fruit, lobes ovate, ovate-lanceolate or elliptic, 2–3 by 1 mm, acute, with a black gland below apex. *Corolla* white, pale mauve, or violet, or only tip of lobes pink, tube c. 2 mm long, finely papillate inside, lobes ovate-lanceolate or elliptic, 2–3 by 1–2 mm, obtuse, glabrous; fornicies

indistinctly bilobed, 0.5 mm wide, 0.2 mm long, ciliolate. *Stamens* very short, 0.5–0.8 mm, anthers 0.5 mm, ovoid. *Pistil*: style c. 1 mm long. *Nutlets* 7–10, pyriform, c. 0.8 mm long, dorsally rounded, brownish grey or blackish brown, smooth, shiny, rarely dorsally with few hairs. — **Fig. 16f.**

Distribution — *Malesia*: New Guinea, endemic.

Habitat — Open, wet places, sometimes in a light shade, in grassy clearings in forests, at forest edges, creek banks, etc., 1400–3350 m altitude.

Note — Type species of the monotypic genus *Zoelleria*, which was described for the increased number of nutlets, but is not distinct from *Trigonotis* (species formerly included in *Havilandia*) in any other character.

15. *Trigonotis robusta* (I.M. Johnston) I.M. Johnston

Trigonotis robusta (I.M. Johnston) I.M. Johnston, J. Arnold Arbor. 21 (1940) 62; Van Royen, Pac. Sc. 29 (1975) 91; Alpine Fl. New Guinea 4 (1983) 3112. — *Havilandia robusta* I.M. Johnston, J. Arnold Arbor. 16 (1935) 191. — Type: *Brass* 5681 (A holo), Papua New Guinea, Mt Albert Edward.

Large, lax herbs often growing in large groups. Stems more or less ascendent, up to 30 cm high, with few branches and lower leaves already withered at flowering time, appressed antrorse strigose. *Leaves* spatulate, spatulate-oblong to oblong, petioles 0.5–1.2 cm long, blade 1.5–4.5 by 0.4–0.7 cm, obliquely truncate at base, rounded or retuse at apex, with 3 nerves on either side of midrib and 2 basal ones, sparsely antrorse strigose in distal part above, with only few hairs, more numerous only along midrib below. *Flowers* solitary in axils of upper leaves. *Calyx* 5–6 mm long, lobes 4–6 by 1–1.5 mm, narrowly lanceolate to elliptic, acute, with a black gland below apex, antrorse strigose along midrib and margins. *Corolla* pink or blue, throat white, or entirely white, or white with blue tips, up to 9 mm long, 12 mm diam., tube 4–6 mm long, lobes broadly spatulate-obovate, 4–6 mm wide, papillate on the inner side; fornicies kidney-shaped, 0.5–1 mm wide, ciliolate. *Stamens* c. 1 mm long, the anthers 0.8 mm long. *Pistil*: style 1–1.5 mm long. *Nutlets* angulate-ovoid, c. 1 mm long, dorsally rounded, with sharp angles, dull grey, finely papillate.

Distribution — *Malesia*: Papua New Guinea, endemic.

Habitat — Wet places in grasslands, along rivulets, 2000–3680 m altitude.

16. *Trigonotis subrosulata* Riedl

Trigonotis subrosulata Riedl, Blumea 38 (1994) 464. — Type: *Mc Gregor* BS 19575 (L holo), Luzon, Mt Polis.

Base not known, but obviously more or less decumbent. Stems erect or ascending, 12–17 cm high, simple or branched at the very base, with subrosulate leaves, densely covered by patent hairs turning fulvous when dry in the lower part, appressed antrorse strigose with white hairs in upper part. *Leaves* oblong to elliptic, lanceolate-oblong or obovate-oblong, petiole 0.5–2.5 cm long, distinctly winged, with dense, long, patent hairs along the margin, blade 2–7 by 0.7–2.2 cm, rosetta leaves tapering gradually into

petiole at base, the single leaf of flowering stems sessile with broadly rounded base or semi-amplexicaulous, long acuminate at apex, lateral nerves indistinct, upper side dark green with often fairly lax, appressed, in the lower half irregularly directed, in the distal part antrorse hairs, lower side pale with antrorse hairs especially dense on midrib and along margins. *Cymes* always paired, terminal or on lateral branches arising from near base, bractless, either naked in lowermost part or with a single flower in the axil between two cymes and with more flowers in their whole length; pedicels 0.5–3 mm long, that of axillary flower up to 5 mm, densely strigose. *Calyx* 2.5–3 mm in flower, up to 4.5 mm in fruit, lobes 2–2.5 by 0.8 mm in flower, 3–3.5 by up to 1.1 mm in fruit, ovate-lanceolate, acute, antrorse strigose especially at base, along midrib and margins. *Corolla* white, 4 mm long, tube c. 2 mm long, lobes suborbicular, broadly rounded, c. 2 mm wide, glabrous; fornicies c. 0.8 mm wide, 0.3 mm long, finely papillate. *Stamens* c. 1 mm long, anthers 0.8 mm, oblong, protruding from throat. *Pistil*: style c. 1 mm long, stigma distinct. *Nutlets* tetrahedral, c. 1 mm long, blackish brown, smooth, shiny, angles costate, ribs light brown.

Distribution — *Malesia*: Philippines (N Luzon). Only known from the type-collection.

Note — Closely related to *T. philippinensis* and *T. oblita*, from which it differs by the patent hairs growing fulvous in the lower part of the stems, from the former, which grows in the same area of Luzon, especially by the nearly rosulate, larger leaves, the winged petioles with dense, patent hairs, the longer calyx with narrower lobes and the light brown ribs of the nutlets.

17. *Trigonotis vestita* P. Royen

Trigonotis vestita P. Royen, Pac. Sc. 29 (1975) 85; Alpine Fl. New Guinea 4 (1983) 3102. — Type: *Lam* 1658 (L holo), Irian Jaya, Mt Doorman.

Small, erect or ascendent herb. Stems up to 25 cm high, branched, the stems and branches glabrous, with leaves confined to the youngest parts, lower down with remnants of old leaves. *Leaves* close to each other, lanceolate, base widening into a sheath-like part, 1–2.2 by 0.15–0.3 cm, often curved downwards, acute, truncate and thickened at the very apex, one-nerved, subappressed strigose along margins only with longer hairs towards the base. *Cymes* axillary, 4–6-flowered, scorpioid while young, straight later on, usually with 1 or 2 bracts; peduncles, rhachis and pedicels angulate, appressed strigose; pedicels 3–6 mm long, in fruit curving downwards. *Calyx* 3.5–4 mm long, divided to the base, lobes elliptic, 1.5(–2) mm wide, obtuse, antrorse strigose along midrib and margins only, with a black gland below the apex. *Corolla* white, glabrous, 4–5 mm long, tube 2–2.5 mm long, lobes broadly obovate, rounded; fornicies kidney-shaped, c. 1 mm wide, 0.5 mm long, papillate. *Stamens* c. 1 mm long, anthers 0.5 mm. *Pistil*: style c. 0.5 mm long. *Nutlets* tetrahedral with sharp angles, c. 1 mm long, brown, smooth.

Distribution — *Malesia*: New Guinea. Known only from the type locality.

Habitat — In swampy places between ferns and grasses in alpine grasslands, 3200–3520 m altitude.

DUBIOUS GENUS

CRUCICARYUM

Crucicaryum O. Brand in Diels, Bot. Jahrb. 62 (1929) 489; P. Royen, Pac. Sc. 29 (1975) 96. — Type species: *Crucicaryum papuanum* O. Brand.

Small, erect herbs, stems appressed villose. *Leaves* lanceolate, upper ones sessile, lower ones unknown. *Inflorescences* subthyrsoidal cincinni, bracteate. *Flowers* numerous, stalked. *Calyx* 5-lobed (?), widely cylindric, lobes ovate, throat-scales 5 (?), semi-lunate. *Stamens* 5 (?), inserted in tube. *Carpels* 4, connate at base only to the style; style shortly claviform. *Receptacle* flat, indistinct. *Nutlets* plano-compressed, shortly hairy with hooked hairs, horizontally spreading.

Distribution — A monotypic genus, endemic in New Guinea.

Note — Nothing is known of this genus except the original description translated into English with slight alterations by Van Royen. His text is followed here word for word. Van Royen's suspicion that it represents a poor form of *Cynoglossum javanicum* (Lehm.) Thunb. (*C. hellwigii* O. Brand in the interpretation adopted in this treatment), may be correct, though it does not explain the flat receptacle and the bracteate inflorescence. However, does Brand's description mean that it is bracteate throughout? Bracts may be present in the lower part of the inflorescence in any case. If there is no stylar column the genus would have to be included in *Lithospermeae* otherwise not represented in the area, or maybe in *Trigonotideae*. No final conclusion can be reached before additional new material becomes known from the alpine zone of the Sarawaket Range in the northeastern part of Papua New Guinea.

Crucicaryum papuanum O. Brand in Diels, Bot. Jahrb. 62 (1929) 489; P. Royen, Pac. Sc. 29 (1975) 96.

Herb. *Leaves* lanceolate, c. 3 by 0.5 cm, acute, sessile. *Pedicels* known in fruit only and as long as calyx. *Sepals* ovate, 1.5–2 mm long. *Corolla* 3 mm long. *Nutlets* orbicular, hardly 1 mm long.

Distribution — Known only from the type collection, Papua New Guinea, Sarawaket Range, 3600–4000 m (*Keysser 41*, destroyed in B).

EXCLUDED GENUS, OF UNCERTAIN AFFINITIES

PTELEOCARPA

Pteleocarpa Oliv., Trans. Linn. Soc. 28 (1873) 515; Ridl., Fl. Malay Penins. 2 (1923) 464; Veldkamp, Fl. Males. Bull. 10, 1 (1988) 47; Ng in Tree Fl. Malaya 4 (1989) 64; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 103. — Type species: *Pteleocarpa malaccensis* Oliv. [= *Pteleocarpa lamponga* (Miq.) Bakh. ex K. Heyne].

Glabrous trees. *Leaves* alternate, lanceolate to ovate-lanceolate. *Inflorescence* paniculoid, many-flowered, terminal, without bracts. *Flowers* on a short stalk. *Calyx* 5-lobed,

imbricate. *Corolla* yellow, with a short tube and 5 oblong, rounded, imbricate lobes sometimes slightly different in size. *Stamens* 5, exserted from the throat, with sagittate anthers. *Ovary* undivided, bilocular, each locule with a small upright and a bigger pendulous ovule; style divided to the base into two branches, each bearing a capitate stigma. *Fruit* broadly elliptic to suborbicular, with a wide, cartilaginous, radially veined wing, one-seeded. *Seed* elongate. — **Fig. 18.**

Distribution — A monotypic genus, see under the species.

Note — The most peculiar features of the genus which clearly show that it cannot be a member of *Boraginaceae* are the radially veined wings of the single fruit and especially the two different ovules, one pendent and one upright. This latter character is very rare in general and found, e.g., in the genus *Maytenus* of *Celastraceae*.

Pteleocarpa was included in *Olacaceae* by its original author, but there are many important differences. Veldkamp, l.c., discusses possible relationships to *Boraginaceae*, *Icacinaeae*, *Olacaceae*, *Cardiopteridaceae*, *Lophopyxidaceae* and *Sapindaceae*, but he arrives at the conclusion that it does not belong to any of them. It may prove necessary to describe a new family for it, the position of which will remain uncertain again, however.

***Pteleocarpa lamponga* (Miq.) K. Heyne**

Pteleocarpa lamponga (Miq.) Bakh. ex K. Heyne, Nutt. Pl. Ned. Indië, ed. 2 (1927) 1309; Veldkamp, Fl. Males. Bull. 10, 1 (1988) 47; Ng in Tree Fl. Malaya 4 (1989) 64; Dayang Awa in Tree Fl. Sabah & Sarawak 2 (1996) 103, f. 4. — *Dodonaea lamponga* Miq., Sumatra (1862) 511. — Type: *Teijsmann s.n.* (BO holo; L), Sumatra.

Pteleocarpa malaccensis Oliv., Trans. Linn. Soc. 28 (1873) 515; Ridl., Fl. Malay Penins. 2 (1923) 464. — Type: unknown.

Pteleocarpa longistyla Becc., Malesia 1 (1877) 130. — Type: unknown.

Tree, up to 30 m high. Trunk 40–60 cm in diam. Bark superficially fissured, yellowish to greenish grey, inner bark pale brown to pale orange, wood pale yellowish to reddish brown; branches reddish brown, youngest, herbaceous shoots minutely papillose. *Leaves* obovate, obovate-lanceolate or lanceolate, petiole 0.7–1 cm long, blade 2.5–10 by 1.2–6 cm, margin entire, base gradually tapering into petiole, apex usually long acuminate, rarely subobtusate to emarginate, 5 or 6 primary nerves on each side of midrib (following the pattern of *Ehretia*), glabrous on upper and lower side. *Inflorescence* terminal, paniculate to thyrsoid-paniculate, with short peduncle, rhachis densely pubescent, flowers numerous; pedicels 2–8 mm long, densely pubescent. *Calyx* campanulate, 1.8–2 mm long, 1.8 mm wide, lobes free for 3/4 of calyx length, ovate to triangular, acute, sometimes imbricate, with few hairs along the margin. *Corolla* yellow, rarely red, tube shorter than calyx, lobes explanate, c. 5 by 1.8–2 mm, obovate-oblong, broadly rounded. *Stamens* inserted at upper end of tube, filaments filiform, about thrice as long as anthers, anthers basifixed, linear, bilobed at base, dehiscent longitudinally, obtuse. *Pistil*: styles 2, 3–4 mm long, filiform, stigmas indistinct; ovary sitting on an ovoid, sterile disc. *Fruit* single, broadly winged, wing suborbicular to ob-

ovate in outline, 3–4.5 cm in diam., fertile locules 2, oblong, 1.3–2 cm long, laterally compressed, wing densely radially veined, slightly emarginate to deeply bifid at apex, continuous also below locules; only the big, pendulous ovule developing into a seed. —

Fig. 18.

Distribution — S Thailand; *Malesia*: Sumatra (incl. Bangka), Malay Peninsula, Singapore, Borneo.

Habitat — Tree of primary lowland and hill forests.

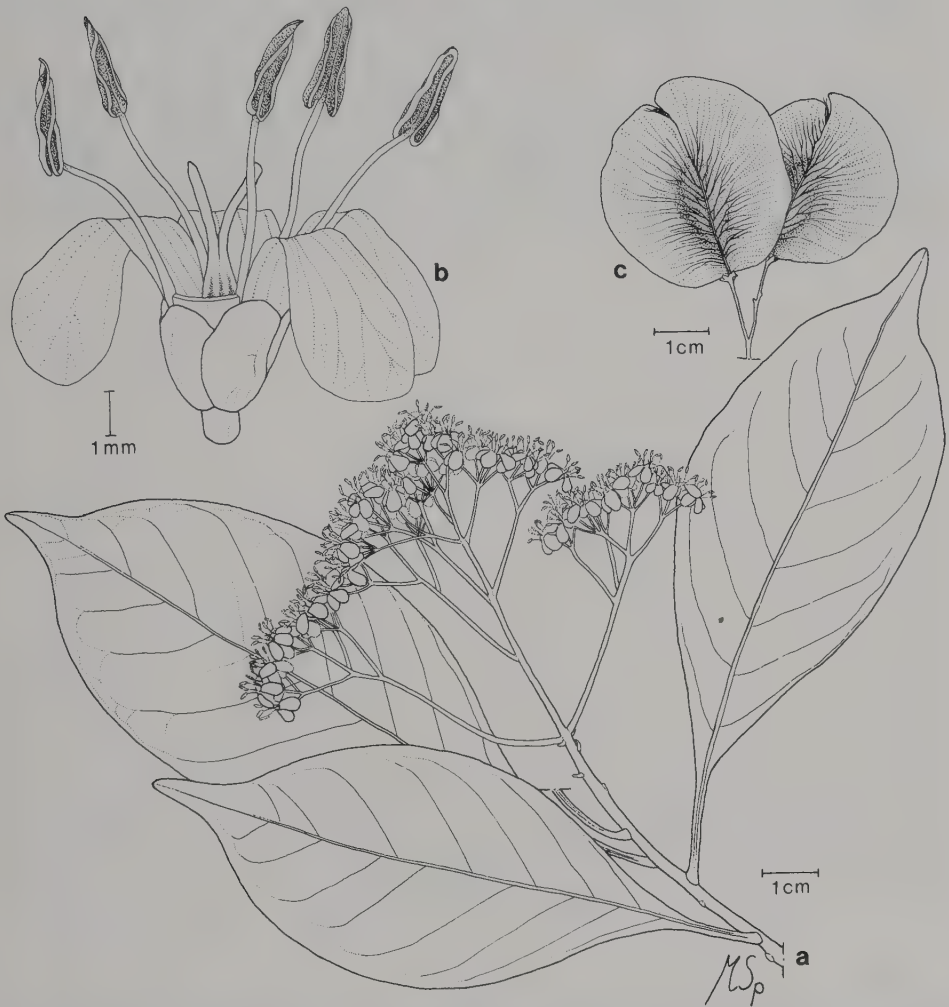


Fig. 18. *Pteleocarpa lamponga* (Miq.) K. Heyne. a. Top of flowering twig; b. flower; c. ripe fruits (a, b: *Lajangah* 44630; c: *Brand SAN* 30871). Drawing M. Spitteler.

DOUBTFUL OR ERRONEOUS RECORDS

Lithospermum zollingeri A.DC., Prodr. 10 (1846) 587. — Type: *Zollinger 352*, Java.

Note — *Lithospermum zollingeri* is a well-defined species from China, that has not been found in Java by anyone since Zollinger. Either it had been introduced there by chance and has vanished long since, or the label data of the type specimen are erroneous.

'*Lithospermum*' *corsonianum* G. Don in Loudon, Gard. Mag. (1842) 371. — Type: *Corson 1839*, Batagoda.

Erect, hispidulous-strigose, branched at apex, with linear leaves and paired, terminal, bracteate spikes, acuminate segments of the calyx and the tube of corolla as long as the calyx. Annual with simple base, 4–5 inches high. Flowers small, yellow.

Note — From the above description, no conclusion as to the identity of the species can be drawn. Certainly it is no *Lithospermum*, as it is far from the area of distribution of that genus. The type specimen had been kept at the Linnean Society in London, but apparently was among those plants that have been sold in 1863. All attempts to locate it have been in vain so far. According to Index Kewensis it came from Timor.

DAPHNIPHYLLACEAE

(Tseng-chieng Huang, Taipei)¹

Daphniphyllaceae Müll.Arg. in DC., Prodr. 16 (1869) 1, nom. cons.

One genus only.

DAPHNIPHYLLUM

Daphniphyllum Blume, Bijdr. (1826) 1153; T.C. Huang, Taiwania 11 (1965) 57–98, 12 (1966) 137–234. — Type species: *Daphniphyllum glaucescens* Blume.

Trees or *shrubs*, evergreen, dioecious. *Leaves* simple, alternate, fasciculate, rarely opposite, subverticillate to verticillate, rarely dimorphic, estipulate; blades elliptic, oblong, obovate to ovate, frequently falcate or oblique, rounded, mucronate, acute to acuminate at apex, rounded, obtuse, acute to cuneate at base, margins entire or revolute, infrequently dentate near the apex, chartaceous, membranous to coriaceous, green or yellow on both surfaces, sometimes shining above, usually glaucous and papillate beneath, midrib frequently impressed above, prominent or not so beneath. *Inflorescences* axillary, rarely subterminal, racemiform, axes angulate, terete or flat, sometimes flexuous; pedicels angulate or flat, rarely pendent; bracts at the base of the inflorescences in 1–several whorls, imbricate, ovate, triangular or linear-ovate or elliptic, usually caducous, sometimes larger than the flower. *Flowers* unisexual. *Calyx* none, or when present 3–6-lobed, with imbricate aestivation, campanulate, cupulate or completely divided when mature, lobes variable in size, shape and margin, rarely larger than the androecium or gynoecium, sometimes articulate, caducous or persistent. *Corolla* absent. *Stamens* in staminate flowers 5–14, free or coherent at apex, subsessile or with long filaments, anthers lunate, oblong, oblong-elliptic, elliptic, broadly elliptic to ovate, compressed or oblique, apex apiculate, triangular, obtuse to emarginate or beaked; staminodia frequently present, rarely articulate, pistillodes rarely present. *Ovary* in pistillate flowers globose to elliptic-globose, imperfectly 2(–4)-septate; each carpel with (1 or) 2 anatropous ovules; placentation suspended or subapical; staminodia on the ovary usually present; style with 1–2(–4) lobes, usually shorter than the ovary, stigmas divaricate, revolute, discoid to circinnate or versatile. *Drupe*s obovoid, elliptic-globose, ovoid to ellipsoid, apex obtuse, base round to obtuse, rarely suddenly constricted at base, shining, smooth, rugose to tuberculate, staminodia frequently persistent, styles usually persistent. *Seed* 1 (or) 2, various in shape and size; germination epigeous; cotyledons two. Chromosome number $2n = 32$ (Huang 1965). — **Fig. 1–8.**

1) With contributions by: P. Baas, Leiden (vegetative anatomy), R.W.J.M. van der Ham, Leiden (pollen morphology), R. Hegnauer, Leiden (phytochemistry). Drawings are by Mrs. Lih-Chiueh Lu, Huang; they were reproduced with permission from Taiwania vol. 12, 1966.

DISTRIBUTION

Forming a monotypic family, *Daphniphyllum* consists of about 30 species, distributed from India to Japan and from Central China to New Guinea, with 16 species in the Malesian region. — **Fig. 1.**

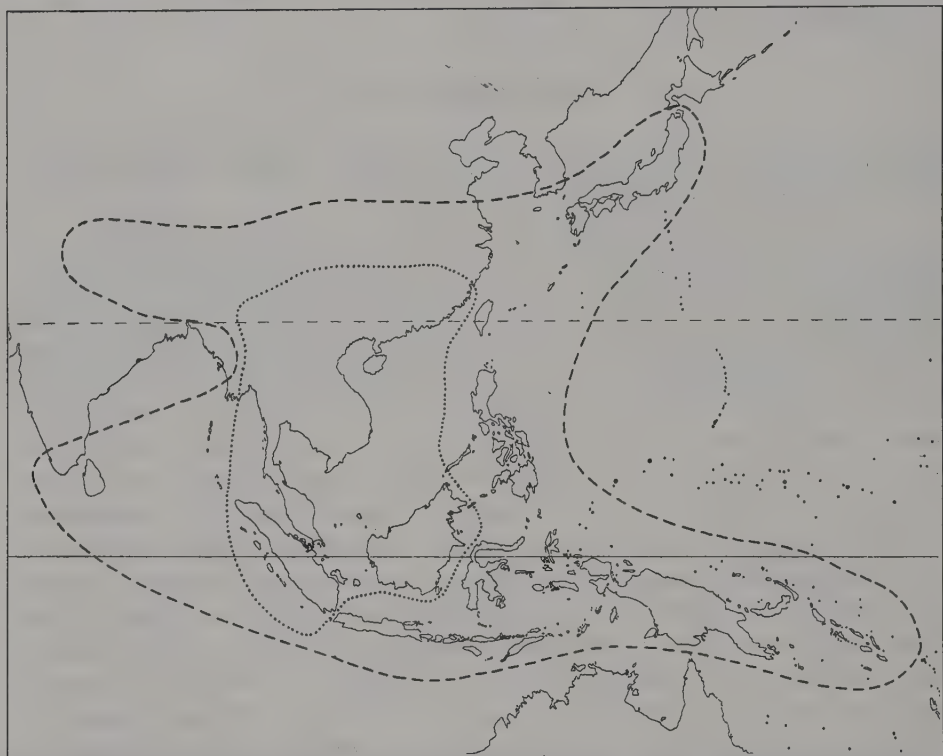


Fig. 1. Distribution map of *Daphniphyllum* and its two sections (----- Section *Daphniphyllum*, Section *Lunata* Huang).

HABITAT

The plants grow on low hillsides, burnt areas, grasslands or montane forests at altitudes from 300 to 4000 m.

VEGETATIVE ANATOMY

(P. Baas)

Leaf anatomy — The leaf anatomy of *Daphniphyllaceae* has been summarized by Metcalfe & Chalk (1950) and Huang (1965). The lamina is dorsiventral. The stomata are paracytic. Epidermal cells are papillate in some species/specimens, depending on their habitat. A hypodermis (or 2-layered epidermis) occurs in *Daphniphyllum gracile* and *D. himalayense*.

Wood anatomy — The wood anatomy has been studied in detail by Carlquist (1982). Gregory (1994) gives a complete bibliography containing 14 more references on *Daphniphyllum* wood structure. The xylem shows many very primitive attributes. Vessels diffuse, solitary, angular in outline, with scalariform perforations with very many (on average 37–96) closely spaced bars. Vessel members are typically long (on average 1000–1890 μm). Lateral vessel wall pits scalariform or transitional. The fibres have distinctly bordered pits in both radial and tangential walls. Parenchyma is scanty paratracheal and diffuse, in c. 7-celled strands. Rays are mostly 1–3-seriate, and strongly heterocellular. Chambered crystals have been reported for *D. glaucescens* var. *glaucescens* only. The anatomical variation within *Daphniphyllum* is limited and related to elevation and latitude (macroclimate). The suite of characters supports affinities of the family with both *Buxaceae* and *Hamamelidaceae* and their closest allies.

References: Carlquist, S., Wood anatomy of Daphniphyllaceae: ecological and phylogenetic considerations, review of pittosporalean families. *Brittonia* 34 (1982) 252–266. — Gregory, M., Bibliography of systematic wood anatomy of dicotyledons. IAWA J., Suppl. 1 (1994). — Huang, T.-C., Monograph of *Daphniphyllum* (1). Taiwan no. 11 (special issue) (1965) 57–98. — Metcalfe, C.R. & L. Chalk. Anatomy of the Dicotyledons 2 (1950) 1241–1243.

POLLEN MORPHOLOGY

(R.W.J.M. van der Ham)

Relatively much has been recorded of the pollen morphology of the *Daphniphyllaceae* and its taxonomic significance. In addition to a number of pollen floras, such as Nakamura (1943), Ikuse (1956), Huang (1967, 1972) and Long (1982), *Daphniphyllum* pollen is treated by Erdtman (1952), Huang (1965), Bhatnagar & Garg (1977), Zavada & Dilcher (1986), Zhang & Lu (1989) and Huang (1996). The last three works mentioned, include scanning electron micrographs, and Zavada & Dilcher (1986) transmission electron micrographs as well.

From the above literature it appears that *Daphniphyllum* is a stenopalynous genus. The tetrad configuration during pollen ontogeny is usually tetrahedral, sometimes isobilateral or decussate. The pollen grains are isopolar 3(–4)-aperturate monads. Grain size is 10–26 μm . Grain shape is oblate to prolate ($P/E = 0.74\text{--}1.59$); the higher P/E values are possibly due to the easy invagination of the long colpi, which results in small equatorial diameters (see for example Huang 1965). The equatorial outline is circular to obtusely triangular. The aperture system is colpate (endoapertures not discernible), colporoidate (endoapertures indistinct), or rarely colporate (endoapertures distinct). The colpi are narrow to rather wide. Transmission electron micrographs show a 0.5 to 0.9 μm thick tectate-columellate exine, in which the sexine is as thick as or thicker than the nexine. The mesocolpial nexine consists of a thick foot layer and a thin endexine; towards the colpi the latter thickens considerably, while the foot layer thins out. The ornamentation is irregularly perforate to more or less fossulate, showing diversely shaped perforations to elongate sinuous depressions. The colpus membranes are rather densely scabrate.

Huang (1996; see also 1965) distinguished two pollen types in *Daphniphyllum*: one for section *Lunata*, with small perforate pollen grains, and another for section *Daphniphyllum*, with larger fossulate grains.

Daphniphyllaceae pollen, being a simple 3-aperturate dicotyledonous pollen type, does not provide the unambiguous clue to the systematic position of the family. Although Erdtman (1952) stated that more or less similar pollen occurs in the *Euphorbiaceae* and that *Hamamelidaceae* pollen is different, several others stressed the dissimilarities comparing with *Euphorbiaceae* pollen, while indicating affinities with the *Hamamelidales* or *Hamamelidaceae* (Huang 1965; Bhatnagar & Garg 1977; Zhang & Lu 1989). Cluster analyses of the *Hamamelidae* by Zavada & Dilcher (1986), exclusively using palynological features, group the *Daphniphyllaceae* together with the *Leitneriaceae*, *Fagaceae* and *Barbeyaceae*. In a cladistic analysis of the pollen morphology by the same authors these families, together with several others, take an intermediate position between the lower and the most derived *Hamamelidae*. They conclude that in order to reach a finer resolution additional non-palynological evidence has to be used.

References: Bhatnagar, A.K. & M. Garg, *Phytomorphology* 27 (1977) 92–97. — Erdtman, G., *Pollen morphology and plant taxonomy* (1952). — Huang, T.C., *Taiwania* 11 (1965) 57–98; *Taiwania* 13 (1967) 15–110; *Pollen flora of Taiwan* (1972); *Blumea* 41 (1996) 231–244. — Ikuse, M., *Pollen grains of Japan* (1956). — Long, H., *Daphniphyllaceae*. *Angiosperm pollen flora of tropic and subtropic China* (1982) 115. — Nakamura, J., *Science Rep. Tôhoku Imp. Univ., Biol.* 17 (1943) 491–512. — Zavada, M.S. & D.L. Dilcher, *Ann. Missouri Bot. Gard.* 73 (1986) 348–381. — Zhang, Z.Y. & A.M. Lu, *Acta Phytotax. Sinica* 27 (1989) 17–26.

PHYTOCHEMISTRY AND CHEMOTAXONOMY

(R. Hegnauer)

This monogeneric family is still a taxon incertae sedis. Bentham & Hooker (according to Radcliffe-Smith 1987) placed *Daphniphyllum* in *Euphorbiaceae*–*Phyllanthaceae* between *Aporosa* and *Baccaurea*. Müller Argoviensis created a separate family for the genus. *Daphniphyllaceae* subsequently were accepted by most authors, but in recent time taxonomists are inclined to favour relationships of *Daphniphyllaceae* with *Hamamelidaceae* rather than with *Euphorbiaceae* (see, e.g., Mabberley 1987; Sutton 1989).

Chemical investigations of *Daphniphyllum* were started by Greshoff who isolated and described the alkaloid daphniphylline from *D. laurinum* [as *D. bancanum* Kurz] (see Hegnauer 1990). Hitherto three classes of secondary metabolites with some promise for plant classification became known in this genus.

Alkaloids — All species investigated contain daphniphylline-like compounds which represent a new type of alkaloids biogenetically derived from the aliphatic triterpene squalene. Daphniphylline itself possesses a polycyclic C₃₀-skeleton. Other *Daphniphyllum* alkaloids are basic octa- or nonanortriterpenoids such as daphnilactone-B (C₂₂-skeleton) and yuzurine (C₂₁-skeleton). A possible biogenetic pathway leading from squalene to protodaphniphylline and daphniphylline was recently proposed (Heathcock et al. 1992). The noralkaloids of *Daphniphyllum* originate by losing eight or nine C-atoms of a terminal geranyl rest not participating in cyclisations.

Iridoid glucosides — The biogenetically related secondary metabolites asperulin and daphylloside have been isolated from leaves of *D. macropodum* Miq.; asperulin was also detected in leaves of *D. laurinum*.

Leaf phenolics — One isolation of a flavonoid glycoside (rutin) was reported long ago in literature. Moreover, screenings of hydrolized leaf extracts yielded paperchromatograms indicating low amounts of the flavonol quercetin and appreciable amounts of the flavones apigenin and luteolin and absence of proanthocyanidins and gallic and ellagic acids, i.e. of both main types of tannins (Hegnauer 1966; Gianassi 1986).

Other chemical characters often useful in classification are:

Storage products of seeds — As far as is known, *Daphniphyllum* seeds store much protein and fatty oil, but lack starch.

Aluminium — Investigating leaves of nine *Daphniphyllum* species Chenery (1948) detected aluminium accumulation in five of them.

Chemotaxonomy — Chemical characters are not yet very helpful in tracing affinities of *Daphniphyllum*. Synthesis and accumulation of asperulin-type iridoids which are probably synthesized along the same pathway as monotropein (Jensen 1991) occurring in *Liquidambar* (*Hamamelidaceae* s.l.) support those taxonomists who stress relationships with *Hamamelidaceae*. Accumulation of aluminium in leaves and the recent isolation (Chenery 1948) of the daphniphylline-type alkaloid (-)-bukittinggine, $C_{22}H_{31}NO_2$, from leaves of *Sapium baccatum* growing in West Sumatra accentuate similarities between *Daphniphyllum* and some *Euphorbiaceae*. Last but not least, the seeming absence of tannins from leaves does not favour either of these two suggestions. Huber (1991) interprets *Daphniphyllaceae* as a possible connecting link between *Hamamelidales* and *Cornales* (and possibly *Bicornes* = *Ericales*); perhaps his arguments would be worth a serious study.

Literature: Chenery, E.M., Kew Bull. (1948) 173–183, *Daphniphyllum* under *Euphorbiaceae* on p. 180. — Gianassi, D.E., Phytochemical aspects of phylogeny in Hamamelidae. Ann. Missouri Bot. Gard. 73 (1986) 417–437. — Heathcock, C.H., et al., J. Org. Chem. 57 (1992) 2554–2566. — Hegnauer, R., Chemotaxonomie der Pflanzen 4 (1966) 9–11, 445, 501; 8 (1989) 376–379. — Hegnauer, R., in: P. Baas et al. (eds.), The plant diversity in Malesia (1990) 101. — Huber, H., Angiospermen. Leitfaden durch die Ordnungen und Familien der Bedecktsamer (1991) 137. — Jensen, S.R., Plant iridoids, their biosynthesis and distribution in Angiosperms, in: J.B. Harborne & F.A. Tomas-Barberan, Ecological chemistry and biochemistry of plant terpenoids (1991) 133–158. — Mabberley, D.J., The plant-book (1987). — Radcliffe-Smith, A., Segregate families from the Euphorbiaceae, in: S.L. Jury et al. (eds.), The Euphorbiales. Chemistry, taxonomy and economic botany. Bot. J. Linn. Soc. 94, 1 & 2 (1987) 47–66 (*Daphniphyllaceae* p. 49). — Sutton, D.A., The Daphniphyllales: a systematic review, in: P.R. Crane & S. Blackmore (eds.), Evolution, systematics and fossil history of the Hamamelidae, vol. 1. Syst. Assoc. Special Vol. 40A (1989) 285–291.

TAXONOMY

Monographic study of *Daphniphyllum* was initiated by Müller Argoviensis (1869), and followed by Rosenthal (1916) and by Huang (1965, 1966). Six species were reported in the Malesian regions in my treatment (Huang 1966), and also three sections were pro-

posed: Section *Lunata* T.C. Huang including *D. laurinum* (Benth.) Baill.; Section *Staminodia* Hurus. including *D. parvifolium* Quisumb. & Merr., and Section *Daphniphyllum* including *D. gracile* Gage, *D. glaucescens* Blume, *D. philippinense* T.C. Huang and *D. woodsonianum* T.C. Huang. Since then, no revision nor monographic treatment has been done for the Malesian region.

Daphniphyllaceae have been placed in various orders (Huang 1965), such as in *Pittosporales* by Thorne (1976, 1983), *Hamamelidales* (Hutchinson 1973; Takhtajan 1980), and *Balanopales* (*Buxales*) (Dahlgren 1983; Thorne 1992). Sutton (1989) and Zhang & Lu (1989) placed it in *Daphniphyllales* with closest relationship to *Hamamelidales* as suggested by Huang (1965) and Cronquist (1983).

The following list provides a summary of the subdivision of the genus according to Huang (1996), with mention of the Malesian species:

Section 1. *Daphniphyllum*

Subsection 1. *Daphniphyllum*

Series 1. *Daphniphyllum* (*D. borneense*, *ceramense*, *dichotomum*, *glaucescens*, *lancifolium*, *luzonense*, *scortechinii*, *sumatraense*, *timorianum*)

Series 2. *Longicalycifera* T.C. Huang (*D. gracile*, *papuanum*)

Series 3. *Unicalycifera* T.C. Huang (*D. buchananiifolium*, *celebense*, *woodsonianum*)

Subsection 2. *Staminodia* Hurus. (*D. parvifolium*)

Section 2. *Lunata* T.C. Huang (*D. laurinum*)

References: Cronquist, A., Some realignments in the Dicotyledons. *Nordic J. Bot.* 3 (1983) 75–83. — Dahlgren, R., General aspects of Angiosperms. Wiley, New York (1983) 65–66, 105, 117–119. — Huang, T.C., Monograph of *Daphniphyllum*, I & II. *Taiwania* 11 (1965) 57–98; 12 (1966) 137–234; Notes on taxonomy and pollen of Malesian *Daphniphyllum*. *Blumea* 41 (1996) 231–244. — Hutchinson, J., The families of flowering plants. 3rd ed, Clarendon Press, Oxford (1983) 229–230. — Müller Argoviensis, J., *Daphniphyllaceae*, in: De Candolle, *Prodromus* 16 (1869) 1–6. — Rosenthal, K., *Daphniphyllaceae*, in: A. Engler, *Pflanzenreich* 68, Fam. IV.147a (1919) 1–15. — Sutton, D.A., The *Daphniphyllales*: A systematic review, in: P.R. Crane & S.S. Blackmore (eds.), *Evolution, systematics and fossil history of the Hamamelidaceae*, 1 (1989) 285–291. Clarendon Press, Oxford. — Takhtajan, A., Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev.* 46 (1980) 225–359. — Thorne, R.F., A phylogenetic classification of the Angiospermae. *Evol. Biol.* 9 (1976) 35–106; Proposed new realignments in the Angiosperms. *Nordic J. Bot.* 3 (1983) 85–117; Classification and geography of the flowering plants. *Bot. Rev.* 58 (1992) 225–348. — Zhang, Z.Y. & A.M. Lu, On the systematic position of *Daphniphyllaceae*. *Acta Phytotax. Sin.* 27 (1989) 17–26, pl. 4 (in Chinese, Engl. summary).

KEY TO THE SPECIES

- 1a. Anthers lunate, introrse, coherent at apex, subsessile; calyx persistent, at least on staminate flowers; drupes strongly tuberculate, usually distinctly glaucous **9. *D. laurinum***
- b. Anthers usually oblong or elliptic, compressed or oblique, extrorse, completely free, with a usually long filament; calyx usually caducous, at least on drupes or absent; drupes smooth to tuberculate, usually not glaucous..... 2

- 2a. Calyx 4–6-lobed; drupes from lustrous and smooth to verrucose or tuberculate; leaf blades usually papillate, chartaceous to coriaceous, all veins prominent and reticulate above. 3
- b. Calyx absent or rarely 1- or 2-lobed, linear, affixed to the base of stamens; drupes usually tuberculate; blades usually epapillate, membranous to chartaceous, all veins obscure and delicate or impressed above. 15
- 3a. Calyx present in both staminate and pistillate flowers 4
- b. Calyx present in pistillate flowers only 14
- 4a. Calyx articulate, caducous and usually longer than the androecium and gynoecium 5
- b. Calyx inarticulate, usually persistent in staminate flowers and shorter than the androecium and gynoecium 6
- 5a. Leaves oblanceolate, oblong, oblong-elliptic to elliptic, usually obtuse, mucronate to rounded at apex and glaucous beneath; mature drupes smooth or lustrous at least in dried specimens; usually growing on upper to subalpine mountain forest or grassland margin **7. *D. gracile***
- b. Leaves lanceolate (narrowly elliptic), acuminate to acute at apex and green beneath; mature drupes tuberculate to verrucose at least in dried specimens, usually growing on lower to middle mountain rain forest **11. *D. papuanum***
- 6a. Blades narrowly oblong, obovate-oblong, obovate, the apex rounded to mucronate or acute at apex, coriaceous, smooth, glaucous and papillate beneath; veins prominently finely reticulate, usually without elevated lateral veins **13. *D. scortechinii***
- b. Blades elliptic to narrowly elliptic, lanceolate to narrowly ovate, usually acute to acuminate or cuspidate at apex 7
- 7a. Leaves elliptic to narrowly elliptic, glaucous, papillate; veins prominent with coarsely elevated reticulation; drupes smooth 8
- b. Leaves narrowly elliptic to lanceolate; veins not with prominently elevated reticulation 9
- 8a. Leaves fleshy, elliptic, base obtuse to cuneate, apex cuspidate to acute to mucronate; drupe stalk 4–10 mm long **1. *D. borneense***
- b. Leaves narrowly elliptic, base cuneate, apex acuminate; drupe stalk 4–5 mm long **5. *D. dichotomum***
- 9a. Blades short, less than 6 cm long; drupes smooth; calyx of staminate flower caducous; veins obscure **4. *D. ceramense***
- b. Blades long, more than 6 cm, shining on both surfaces 10
- 10a. Blades with acute-obtuse base **15. *D. timorianum***
- b. Blades with cuneate base. 11
- 11a. Fruiting pedicels usually more than 1 cm long; styles usually caducous; leaves ovate-lanceolate 12
- b. Fruiting pedicels less than 1 cm long; styles persistent; leaves lanceolate 13
- 12a. Drupes tuberculate and leaves papillate or drupes smooth and leaves epapillate **6. *D. glaucescens***
- b. Drupes smooth and leaves papillate **10. *D. luzonense***

- 13a. Drupes smooth, 4 mm in diameter; leaves papillate, obtuse at base; styles recurved **14. *D. sumatraense***
 b. Drupes rugose, 6–7 mm in diameter; leaves epapillate, acute at base; styles circinnate **8. *D. lancifolium***
 14a. Leaves petiolate, petioles 2–4 cm long; filaments 0.7–0.8 mm long **2. *D. buchananiifolium***
 b. Leaves subsessile, petioles 0.2 mm long; filaments 1.2–2.3 mm long **16. *D. woodsonianum***
 15a. Leaves elliptic, both ends acute, 6–6.5 by 2.5–3 cm **3. *D. celebense***
 b. Leaves oblong-obovate, apex mucronate, cuneate at base, 4–9 by 1–2 cm **12. *D. parvifolium***

1. *Daphniphyllum borneense* Stapf

Daphniphyllum borneense Stapf, Trans. Linn. Soc. II, 4 (1894) 224. — *Daphniphyllum glaucescens* Blume subsp. *borneense* (Stapf) T.C. Huang, Taiwania 12 (1966) 192, f. 33; Perumal in Tree Fl. Sabah & Sarawak 2 (1996) 158. — Type: *Haviland 1070* (K holo; BM, K, L, US).

Shrub or small *tree*, 2–9 m tall, clear bole 0.9–1 m in diam., crown 1.5 m wide, outer bark smooth, grey, slash outer bark green, inner bark coarse, brown like milk chocolate, sapwood whitish to yellow flush. *Leaves* fascicled at tip of branchlets, opposite; blades narrowly elliptic to elliptic, 5–10 by 2.5–4.2 cm, apex cuspidate, acuminate or mucronate, base cuneate, margins entire, coriaceous, brown above, glaucous beneath, lateral veins reticulate or in 8 pairs, elevated on both surfaces, the reticulation especially prominent on upper surface; petiole red-violet or tinged purple, 1.5–3 cm long. *Staminate inflorescences* 4–5 cm long; flowers purple, glaucous, calyx 5-lobed, stamens 6–8; anther red-violet, elliptic, apiculate, 1.5 mm long, 0.8 mm wide; pedicels 7–9 cm long. *Pistillate inflorescences* 4–5 cm long, female flowers glaucous (green) in bud, 5 calyx lobes free, lanceolate, caducous, ovary with several staminodes, stigmas recurved to circinnate; pedicels 4–5 mm long. *Fruiting axes* 4.5 cm long, drupes ellipsoidal, 10–12 mm long, 5–6 mm wide, green turning to red brown, dull red to blackish purple when ripe, smooth; fruit stalks 0.4–1 cm long.

Distribution — *Malesia*: North Borneo and Kalimantan.

Habitat & Ecology — Growing on flat ridges with low forest; stunted dense upper montane rain forest on granodiorite; on cliff faces; ericoid ridge top vegetation; slopes of mossy forest associated with *Talauma* and *Symplocos*, at altitudes of 1500 to 4000 m.

2. *Daphniphyllum buchananiifolium* Hallier f.

Daphniphyllum buchananiifolium Hallier f., Meded. Rijks Herb. Leiden 37 (1918) 13. — *Daphniphyllum glaucescens* Blume subsp. *buchananiifolium* (Hallier f.) T.C. Huang, Taiwania 12 (1966) 192, f. 37. — Type: *Elmer 8538* (A holo; BO, E, L, US).

Daphniphyllum obtusifolium Merr., Philipp. J. Sc. 16 (1920) 552. — Type: *Ramos & Edaño s.n.*, May 1917 (A holo; BO, E, L, US), syn. nov.

Daphniphyllum philippinense T.C. Huang, Ann. Missouri Bot. Gard. 53 (1966) 30, f. 2. — Type: *T. C. Zschakhs 1835* (US holo), syn. nov.

Shrub or tree, up to 10–25 m tall. *Leaves* dimorphic, the earlier leaves very large elliptic, apex rounded or mucronulate, base cuneate to obtuse, 12–14 by 5.5–7 cm, purple or reddish tinged, glaucous beneath, with petioles 3.5–8.5 cm long, hard chartaceous, the later leaves narrowly elliptic, obovate or oblanceolate, apex mucronulate, base cuneate, 4.5–9 by 2.5–2.7 cm, margins revolute, coriaceous, dark green above, lighter beneath, but not glaucous shining; lateral veins 7–9 pairs, thin, slightly prominent on both surfaces, the blades of earlier leaves usually 3 times larger than those of later ones; petioles 1–2.5 cm long. *Staminate inflorescences* flat, c. 3 cm long, green, calyx absent or bracteate, the bracts 1 or 2, free, longer than filaments, or 3 or 4 very short in youth from the base of stamens; stamens 5–7(–11), filaments green 0.2–0.4 mm long, anthers oblong or oblong-elliptic, 0.7–0.8 mm long, yellow, apiculate; pedicels 4–7 mm long. *Pistillate inflorescences* 1.5 cm long, sepals numerous, free, elliptic, mixed with many undifferentiated staminodes, green, ovary purple, styles divaricate, as long as ovary, stigmas greenish elliptic-ovoid, 2 mm long; pedicels 2–4 mm long. *Fruiting axes* angulate, 3–8.5 cm long; calyx caducous, staminodial scars and calyx scars (?) prominent, in 1 or 2 whorls. *Drupe*s ellipsoid, elliptic-globose, 10–15 mm long, 6–8 mm in diam., mostly light green, dull violet or black, smooth or verrucose to tuberculate, soft, somewhat juicy with one large seed when ripe, stigmas divaricate; fruit stalks 0.7–1 cm long.

Distribution — *Malesia*: Philippines (Luzon, Mindanao, Biliran).

Habitat & Ecology — Primary forest of one storey, mossy, bordering open grassland, and on sandy-loamy soil, at altitudes of 2100 to 2800 m.

Note — The type specimens of both *D. buchananii* and *D. obtusifolium* have either drupes or immature drupes without male specimens. After closer examination, I emend the staminate flowers, reduce *D. philippinense*, and treat all these as conspecific taxa.

3. *Daphniphyllum celebense* K. Rosenthal

Daphniphyllum celebense K. Rosenthal in Engl., Pflanzenr. 68 (IV.147a) (1919) 5. — *Daphniphyllum glaucescens* Blume subsp. *celebense* (K. Rosenthal) T. C. Huang, Taiwania 12 (1966) 186. — Type: Warburg 16903 (B, destroyed). Neotype (Huang 1996): Teijsmann 13664 (BO).

Branches slender. *Leaves* with petioles 1.5 cm long; blades elliptic, apex and base acute, 6–6.5 by 2.5–3 cm, margins strongly revolute, rough, coriaceous, upper surface shining, beneath papillose, lateral nerves 7–9 pairs. *Male flowers* unknown. *Pistillate inflorescences* racemes, 3.5–4 cm long, calyx obscure, ovary ellipsoid, staminodia 5 or 6, 1–1.5 cm long, lanceolate, acute, stigmas divaricate; pedicels 10–15 mm long. *Fruits* unknown.

Distribution — *Malesia*: endemic to Celebes (Sulawesi).

Habitat & Ecology — No data available.

Note — According to the original description of Rosenthal (1919), this species is related to *D. macropodum* and *D. himalayense* but differs in the size and form of leaves. For this study, the type specimen (Warburg 16903) was not available because it was destroyed during World War II. I consider it an insufficiently known taxon.

4. *Daphniphyllum ceramense* (T.C. Huang) T.C. Huang

Daphniphyllum ceramense (T.C. Huang) T.C. Huang, Blumea 41 (1996) 237. — *Daphniphyllum glaucescens* Blume subsp. *ceramense* T.C. Huang, Taiwania 12 (1966) 190, f. 32. — Type: *Eyma* 2047 (BO holo; K, L).

Leaves short, narrowly elliptic, apex cuspidate, base acute-obtuse, 4–6 by 1.8–2.5 cm, coriaceous, shining on both surfaces, lateral veins 6 pairs, reticulation fine. *Staminate inflorescences* 2.5–4 cm long, pedicels angulate, 5–7 mm, calyx lobes 4 or 5, linear-ovate, 4/5 as long as androecium, caducous, articulate, stamens 8 or 9, filaments flat-oblong, 2–4 mm, anthers oblong to oblong-ovate, 1.2–1.6 mm long, apiculate. *Pistillate inflorescences* 2–2.5 cm long, calyx lanceolate, two whorls of several free lobes, ovary blue-green, style branches recurved. *Fruiting axes* 2–3 cm long. *Drapes* smooth, ellipsoidal, green, later black purple, 1.3 cm long, 0.7 cm wide; fruit stalk 5 mm long.

Distribution — *Malesia*: Moluccas (Ceram).

Habitat & Ecology — No data available.

Note — The species is similar to *D. borneense* except for having obscure leaf venation and caducous calyces on staminate flowers. The free, lanceolate, two-whorled calyx lobes are very peculiar.

5. *Daphniphyllum dichotomum* (T.C. Huang) T.C. Huang

Daphniphyllum dichotomum (T.C. Huang) T.C. Huang, Blumea 41 (1996) 238. — *Daphniphyllum glaucescens* Blume subsp. *dichotomum* T.C. Huang, Taiwania 12 (1966) 190, f. 31; Perumal in Tree Fl. Sabah & Sarwak 2 (1996) 158. — Type: *Clemens s.n.* & *Suppl.* (US lecto; A, BO, L, NY, UC).

Daphniphyllum reticulatum H. Heine, Feddes Rep. 54 (1951) 232, nom. illeg., non Keng (1951).

Shrub or small *tree*, 7.5 m high, 60 cm in diam., bark smooth, grey, inner bark yellowish, sapwood white yellowish. *Leaves* narrowly elliptic, apex acuminate, base cuneate, 7–10 by 2.2–2.9 cm, coriaceous, green on both surfaces, veins delicately reticulate and prominent on both surfaces, with 4 or 5 pairs of obscure lateral veins; petioles 0.8–2 cm long. *Staminate inflorescences* unknown. *Pistillate inflorescences* 2.5 cm long; calyx 4- or 5-lobed, lobes triangular, caducous, styles recurved or circinnate; pedicels c. 2 mm long. *Fruiting axes* 2.5–4.5 cm long, 1 mm thick. *Drapes* ovoidal, 7 mm long, 6 mm thick without calyx, green and red brown when ripe; fruit stalks 4–5 mm long, 1 mm thick.

Distribution — *Malesia*: Borneo (Sabah).

Habitat & Ecology — Primary forest on limestone cliff and boulders of organic soil at an altitude of 960 m.

Note — This species differs from *D. borneense* mainly by its narrowly elliptic leaves and its occurrence at low elevation. It is closely allied to *D. sumatraense*.

6. *Daphniphyllum glaucescens* Blume

Daphniphyllum glaucescens Blume, Bijdr. (1826) 1153; Müll. Arg. in DC., Prodr. 16 (1869) 3, p. p.; T.C. Huang, Taiwania 12 (1966) 163, f. 23, p. p. — Type: *Blume* 1908 (L holo; L, NY, US).

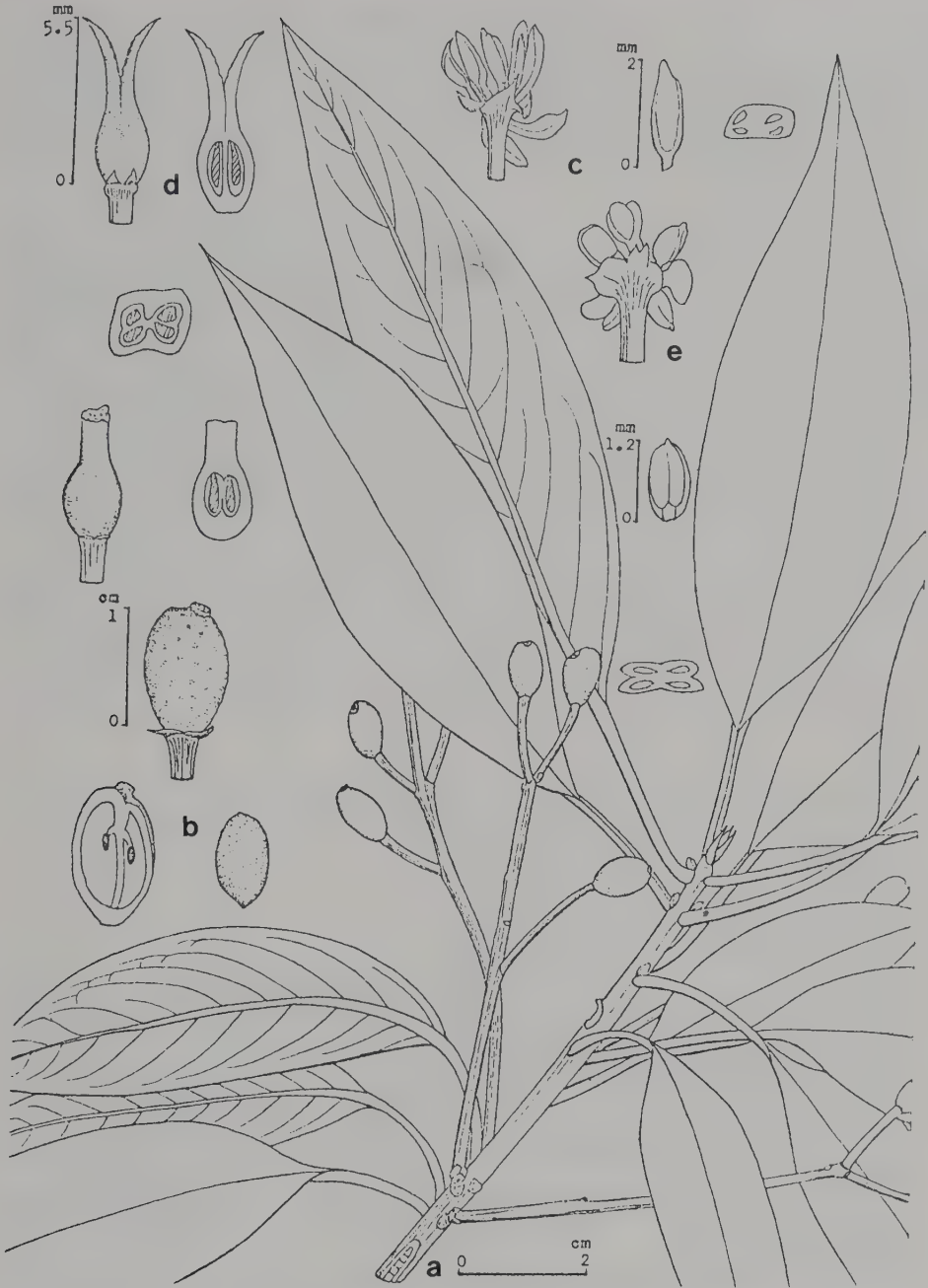


Fig. 2. *Daphniphyllum glaucescens* Blume var. *blumeianum* (Baill. ex Müll. Arg.) J. J. Sm. a. Twig with fruits; b. ovary with longitudinal section, fruit with longitudinal section, and seed; c. staminate flower, stamen and anther in cross section (a, b: Blume s. n.; c: Elbert 2740). — *D. glaucescens* Blume var. *glaucescens*. d. Ovary, longitudinal and cross section; e. staminate flower, stamen and anther in cross section (d: Hasan 1; e: Blume 1908).

KEY TO THE VARIETIES

- 1a. Drupes tuberculate; leaves papillate **a. var. glaucescens**
 b. Drupes smooth; leaves epapillate **b. var. blumeinum**

a. var. glaucescens

Trees, 6–18 m high, 25 cm in diam., crown flattish, outer bark smooth, brown to brownish grey, inner bark dull brown, cream outwards, sapwood brownish white, slash wood hard, cream-yellow. *Leaves* fasciculate; blades lanceolate to narrowly elliptic, apex acuminate to cuspidate, base cuneate, margins slightly revolute, 8–16 by 3–5 cm, firmly chartaceous, darkish green above, greyish brown; glaucous beneath, lateral veins 7–12 pairs; petioles narrowly triangular in section, sulcate above, 1–4.5 cm long, reddish. *Staminate inflorescences* slender, flat, 3–6 cm long; bract caducous; calyx campanulate, 4 or 5 lobes varying as to serration, size and shape; stamens 8–10, filaments oblong, 0.2–0.6 mm long, anthers usually obliquely-lunate, oblong or small broadly elliptic, 0.6–1.5 mm long, strongly apiculate; pedicels 1.5 mm long. *Pistillate inflorescences* angulate, 4–5 cm long; female flowers green; calyx usually caducous; styles recurved or circinnate, as long as the ovary; pedicels terete, 6–10 mm long. *Fruiting axes* angulate, 3.5–6 cm long; bracts caducous. *Drupes* ellipsoid to ovoid, 6–14 mm long, 5–7 mm in diam., apex acute to round, base acute to ovate, tuberculate, green, ripening purple-green with black stigma; styles usually caducous or circinnate; fruit stalks 5–16 mm long. — **Fig. 2d, e.**

Distribution — *Malesia*: Peninsular Malaysia (Perak), Java, Celebes.

Habitat & Ecology — Collected in upper montane forest, at altitudes from 1300 to 2600 m in Java and 1200 to 1700 m in Malaysia.

b. var. blumeinum (Baill. ex Müll. Arg.) J. J. Sm.

Daphniphyllum glaucescens Blume var. *blumeinum* (Baill. ex Müll. Arg.) J. J. Sm. in Koord. & Valetton, Bijdr. Booms. Java 12 (1910) 328. — *Daphniphyllum blumeinum* Baill. ex Müll. Arg. in DC., Prodr. 16 (1869) 3; T. C. Huang, Taiwan 12 (1966) 166, f. 23. — Type: *Zollinger 2140* (P holo). *Daphniphyllum acutifolium* Müll. Arg. in DC., Prodr. 16 (1869) 5. — Type: *Blume s.n.* (L holo). *Daphniphyllum zollingeri* Müll. Arg. in DC., Prodr. 16 (1869) 2. — Type: *Zollinger s.n.* (BO, L, P).

This variety differs from the typical variety only by its shining leaf surfaces and the smooth drupes. — **Fig. 2a–c.**

Distribution — *Malesia*: Peninsular Malaysia (Perak), Java, Lesser Sunda Islands (Bali, Lombok), Celebes.

Habitat & Ecology — Collected at altitudes of 1300 to 1700 m.

7. *Daphniphyllum gracile* Gage

Daphniphyllum gracile Gage, Nova Guinea 12 (1917) 480; T. C. Huang, Taiwan 12 (1966) 155, f. 22; Barker in Handb. Fl. Papua New Guinea 2 (1981) 34. — Type: *Pulle 2439* (L lecto; BO).



Fig. 3. *Daphniphyllum gracile* Gage var. *gracile*. a. Twig with pistillate flowers; b. ovary showing a staminodium and calyx scars, with longitudinal and cross section; c. fruit with longitudinal section and seed; d. fruit; e. staminate flower, stamen, and anther in cross section; f. staminate flowers with pistilodes (a: Pulle 2439; b, c: Hoogland & Pullen 5730; d: Brass 12632; e: Robbins 425; f: Darby 354). — *D. papuanum* Hallier f. var. *tuberculatum* (T.C. Huang) T.C. Huang. g. Fruit (Robbins 880).

KEY TO THE VARIETIES

- 1a. Leaves thick, coriaceous **a. var. gracile**
 b. Leaves thin, semi-coriaceous **b. var. newirelandum**

a. var. gracile

Small slender *trees* or *shrubs* of lower storey or-becoming part of canopy, up to 22 m high, bole up to 45 cm in diam. Bark grey or grey-brown with vertical fissures, sub-smooth, greenish, white laterally on lenticellate ridges, blaze pale greenish white, brown or dark pustular and horizontally ridged, undersurface orange green, middle bark green and red, inner bark light brown, straw brown, white or pinkish, cream, light orange-brown and red mottled, slash 5 mm thick, underbark orange, brownish green to reddish brown with light green to white lines; wood white, very light brownish white or straw-coloured with very fine rays of yellow, red below, moderately hard to soft. *Leaves* alternate to fasciculate; blades from elliptic, narrowly elliptic to obovate, sometimes slightly oblique, 4–20 by 1.2–7.5 cm, apex mucronulate to mucronate, sometimes cuspidate, base cuneate to obtuse, margins revolute, firmly chartaceous or subcoriaceous, shining brown or green on both surfaces, papillate and frequently glaucous beneath or purplish green or light green tinged with purple in young leaves, dark yellow-green, or olive green in old leaves, lateral veins 7–14 pairs, impressed above, slightly ascending below, dark reddish purple or red on the lower side of midrib; petiole triangular, sulcate above, articulate, red, whitish grey or silvery, 1–15 cm long. *Staminate inflorescences* 3–7 cm long, calyx 4–6-lobed, lobes narrowly elliptic, free, entire or with serrulate apex, 1.5 mm long, longer than androecium, caducous, articulate, greenish, purple, dark purplish red, brown, or closed stamens reddish purple, open ones dark brown, stamens 5–8, anthers purple, purplish blue, pruinose, violet-purple in bud, filaments oblong, 0.2–1 mm long; pedicels terete, 2–12 cm long. *Pistillate inflorescences* flat, 3–5 cm long, 0.8 mm wide, bluish-purple flower buds subtended by pale green bracts; calyx 4–6-lobed, linear to elliptic, 1–6 mm long, longer than gynoecium, caducous, articulate (called glands by Gage), greenish purple, greenish cream, ovary bluish green or greyish purple, staminodia green, tinged with violet-purple in bud, styles divaricate, stigmas recurved, dark or red; pedicels flat, 2–12 cm long, green; bracts narrowly elliptic, 3 mm long, partially persistent. *Fruiting axes* angulate, 2–8.5 cm long, red; calyx caducous. *Drupe*s lustrous, ovoid or elliptic globose, 5–11 mm in diam., rounded on both ends, young drupes glaucous, green, olive green or yellow green turning purple, red, dark purple blue, reddish purple, brown or black at maturity; style divaricate, staminodial scars persistent; fruit stalks angulate, 4–15 mm long, 1 mm wide. — **Fig. 3a–f, 4, 5.**

Distribution — *Malesia*: Celebes (rare), New Guinea.

Habitat & Ecology — In montane and subalpine forest, shrubland and grassland, at altitudes between 1300 and 3300 m. Frequently associated with *Nothofagus* and *Phyllocladus* in ridge forest, *Nothofagus*–*Castanopsis* forest on old, well-drained volcanic soil; *Papuacedrus* and *Olearis* in grassland, or *Xanthomyrtus*, *Papuacedrus*, *Quintinia*, *Ericaceae* in alpine shrubland.



Fig. 4. *Daphniphyllum gracile* Gage. Top of twig with staminate inflorescences (van Royen 11086). Mt Amungurwa, Papua New Guinea, c. 3000 m altitude. Photo P. van Royen, 13 June 1976.



Fig. 5. *Daphniphyllum gracile* Gage. Pistillate inflorescences (van Royen 10911). Track from Iswan swamp to Rock Pile, Papua New Guinea, 3200 m altitude. Photo P. van Royen, 21 May 1976.

Note — The collection of *Streimann & students 27812* possesses two kinds of leaves which are very important characters to distinguish plants of *D. gracile* and *D. papuanum*. The young leaves in the female vegetative branches bear oblanceolate leaves with acute or cuspidate apex but leaves on the fruiting branches bear lanceolate leaves with acuminate apex and smooth drupes. The young leaves agree with those of var. *gracile* and the old leaves and mature drupes agree with those of *D. papuanum* var. *tuberculatum*. Possibly they are ecotypes.

b. var. *newirelandum* T.C. Huang

Daphniphyllum gracile Gage var. *newirelandum* T.C. Huang, *Blumea* 41 (1996) 239, f. 2. — Type: *Gideon s.n.* (CANB holo).

Shrubs, c. 3 m high, with a round crown. *Leaves* oblong-elliptic, apex obtuse, cuspidate or mucronate, base obtuse, 6.5–10 by 2.5–4 cm, margins revolute, semi-coriaceous, lateral veins 7 pairs, membranous. *Flowers* unknown. *Fruiting axes* 2.5 cm long, calyx narrow, caducous, styles short, divaricate, caducous. *Drupes* green, ellipsoidal, 8–10 mm long, 7–8 mm in diam., smooth to verrucose.

Distribution — *Malesia*: Bismarck Archipelago, New Ireland, endemic. Two specimens known, both from subprov. Konos.

Habitat & Ecology — Collected on top of a small hill dominated by *Gleichenia* which is continuously burnt, at an altitude of 980 m.

8. *Daphniphyllum lancifolium* Hook. f.

Daphniphyllum lancifolium Hook. f., *Fl. Brit. India* 5 (1887) 354. — *Daphniphyllum glaucescens* Blume subsp. *lancifolium* (Hook. f.) T.C. Huang, *Taiwania* 12 (1966) 165, f. 30. — Type: *King's Coll. 7007* (K holo; BM, L).

Trees, 12–18 m high. *Leaves* narrowly angular, ovate, apex acuminate, base cuneate, 12–13.5 by 3.5–4 cm, margins slightly revolute, coriaceous, lateral veins delicate, c. 10 pairs, elevated on both surfaces, reticulation obscure; petioles 3.5 cm long. *Flowers* unknown. *Fruiting axes* 7 cm long. *Drupes* ellipsoidal, 1 cm long, 8 mm in diam., rugose to tuberculate, styles circinnate, caducous, calyx caducous, fruit stalks 5 mm long.

Distribution — *Malesia*: Malay Peninsula, only known from type specimen, collected in Perak, Gunong Ejong.

Habitat & Ecology — Under dense pine forest, at unknown altitude.

Note — This species differs from *D. glaucescens* by its shorter fruit stalks. It also can be distinguished from *D. dichotomum* by its larger tuberculate drupes.

Fig. 6. *Daphniphyllum laurinum* (Benth.) Baill. a. Twig with fruits; b. ovary, longitudinal and cross sections, and calyx; c. fruit and longitudinal section, and seed; d. tricarpellate fruit, cross section and top view; e. bicarpellate fruit with a staminodium and top view; f. staminate flower and a second staminate flower with a pistillode; g. stamen, anther in cross section and staminate calyx (a, c, g: Wallich 1836; b: Hervey s.n.; d: Clemens 30674; e: Scortechini s.n.; f: Wallich 1836 and Creagh s.n.).



9. *Daphniphyllum laurinum* (Benth.) Baill.

Daphniphyllum laurinum (Benth.) Baill., Étud. Gen. Euph. (1858) 565, t. 21; T.C. Huang, Taiwania 12 (1966) 139, f. 13. — *Goughia laurina* Benth. in Hook., Kew J. 6 (1854) 9. — Type: Wallich 1836 (K lecto; BM, E, K).

Daphniphyllum bancanum Kurz in Teijsm. & Binn., Pl. Nov. Hort. Bogor. Cult., Nat. Tijds. Ned. Ind. 27 (1864) 51. — Type: Teijsmann s.n. (BO, US).

Shrubs or small *trees*, up to 21 m high, 30 cm in diam., outer bark smooth or lenticellate, red or red-grey, inner bark red or yellow, fibrous, soft, cambium white. *Leaves* alternate or fasciculate; blades large, narrowly elliptic to lanceolate, apex acuminate or falcate, base cuneate or obtuse, 11–37 by 3.5–13 cm, margins remotely undulate, firmly chartaceous, brown on both surfaces, sometimes papillate and glaucous beneath, lateral veins 10–12 pairs, obscure, midrib triangular, impressed above; petioles terete or triangular, 3–21 cm long. *Staminate inflorescences* terete, 1–9 cm long, 0.5 mm wide; flowers cream-coloured, white or whitish green, 1–1.5(–2.5) mm long, calyx 3- or 4- (or 7–10-)lobed, united basally, lobes broadly triangular, unequal, serrate, usually half as long as stamens, stamens 8 or 9, the filaments broadly oblong, 0.4 mm long, anthers lunate, non-beaked, 0.3 mm long, rarely pistillodes present; pedicels terete, 5–20 mm long, pinkish; bracts caducous. *Pistillate inflorescences* terete, finely grooved, 2–4.5 cm long, calyx discoid or campanulate, 4- or 5-lobed, lobes triangular, unequal, reflexed, united at base, greenish, persistent; pedicels 0.7–1.6 cm long. *Fruiting axes* 2–8.5 cm long, 1 mm wide. *Drapes* elliptic-obovoid, elliptic-globose, or obovoid, 0.7–1.2 cm long, 5–7 mm in diameter, faintly glaucous, pale green, green, or white when young, brown when ripe, tuberculate, styles very short, divaricate, staminodia rarely present, calyx persistent; fruit stalk 0.4–1.6 cm long. — **Fig. 6.**

Distribution — *Malesia*: widely distributed in Peninsular Malaysia and Borneo, also in Sumatra and Bangka, cultivated in Java, derived from specimens in the Botanic Garden, Bogor.

Habitat & Ecology — It has been collected on low undulating hillsides, on the summit of limestone hills with exposed porphyritic rocks; in secondary forest; in high jungle crests at altitudes of 500–900 m; on alluvial riverbanks; on flat land, and in mixed low-land forests.

Uses — A decoction of the roots is used in Bangka (Indonesia) as a medicine against diarrhoea and thrush.

Note — Two different types of leaves are observed on different specimens; one is lanceolate with a obtuse or cordate base and the other is narrowly elliptic with a cuneate base.

10. *Daphniphyllum luzonense* Elmer

Daphniphyllum luzonense Elmer, Leaflet Philipp. Bot. 1 (1908) 309, excl. specim. Elmer 8538 (= *D. buchananifolium*). — *Daphniphyllum glaucescens* Blume subsp. *luzonense* (Elmer) T.C. Huang, Taiwania 12 (1966) 188, f. 35. — Type: Elmer 8615 (L neo; A, BO, E, K, MO, NY).

Small *trees*, 10 m high, 15 cm in diam., twigs smooth, lenticels light brown. *Leaves* narrowly elliptic to narrowly oblong, apex acuminate, base obtuse, 12–15 by 3.8–5 cm,

the margins undulate, shining, thin submembranaceous; veins 5–8 pairs, prominent, ascending above; stipules caducous, glaucous, sharply acuminate, papillate below; petioles reddish, 2.5–5 cm long. *Staminate inflorescences* unknown. *Pistillate inflorescences* axillary, racemose, 3.5–10 cm long; pistillate flowers sessile, subtended by 4 bracts, ovary ovoid or ellipsoid, glaucous, smooth, styles short, glaucous, stigmas circinnately 2-lobed. *Fruiting axes* 6–7 cm long (?). *Drupes* ellipsoid, 9–15 mm long; pedicels umbellately clustered at apex, 1–1.5 cm long, glabrous, subtended by minute caducous bracts.

Distribution — *Malesia*: Philippines (Biliran, Luzon, Mindoro, Mindanao, Palawan).

Habitat & Ecology — On forested slopes at an altitude of about 1500 m.

Uses — It is used for curing poisoned persons by eating bark and fruit to enhance vomiting. A decoction of drupes and leaves is used to treat stomach aches and also as a poison antidote. Wood used for fuel and construction.

11. *Daphniphyllum papuanum* Hallier f.

Daphniphyllum papuanum Hallier f., Meded. Rijks Herb. Leiden 37 (1910) 13. — Type: W.A. Sayer 1887 (L holo).

KEY TO THE VARIETIES

- 1a. Drupes smooth to verrucose **a. var. *papuanum***
- b. Drupes tuberculate **b. var. *tuberculatum***

a. var. *papuanum*

Slender understorey tree, 4–25 m high, 20–30 cm in diam., outer bark grey-brown, quite smooth, inner bark straw-coloured, flecked with brown; branches thick, lenticels elliptic. *Leaves* fascicled at the tip of branches; blades lanceolate, acuminate at apex, the acumen 5–15 mm long, cuneate at base, 12.5–20 by 3.5–7.5 cm, bright brown on both surfaces, lateral nerves 12–14 pairs, prominent on both surfaces, ascending above, subtrinnerved at base; petioles 4–5 cm long, black. *Staminate flowers* not seen. *Pistillate inflorescences* 6 cm long; calyx caducous; stigmas circinnate; pedicels 9–13 mm long. *Fruiting axes* solitary, axillary, racemose, c. 10 cm long; calyx obscure. *Drupes* more or less ellipsoid, dark brown, nearly verrucose, c. 1 cm long, 7 mm wide; stigmas 2, persistent, recurved, terminal, subsessile; fruit stalks 7–12 mm long.

Distribution — *Malesia*: widely distributed in New Guinea.

Habitat & Ecology — In *Nothofagus*–*Castanopsis* or *Agathis* forests in upper mid-mountain rain forest, at altitudes of 850 to 1860 m.

b. var. *tuberculatum* (T.C. Huang) T.C. Huang

Daphniphyllum papuanum Hallier f. var. *tuberculatum* (T.C. Huang) T.C. Huang, Blumea 41 (1996) 240. — *Daphniphyllum gracile* Gage var. *tuberculatum* T.C. Huang, Taiwania 12 (1966) 159, f. 22E; Barker in Henty, Handb. Fl. Papua New Guinea 2 (1981) 37, excl. specim. W.A. Sayer 1887. — Type: Brass 13705 (A holo; BO, L).

Shrubs or small *trees* in understorey, 3–15 m high, 2–24 cm diam., outer bark grey or brown, large pustular, brown green, scrape green, inner bark light brown, yellow, blaze amber yellow, sap staining wood yellow, wood cream, white or straw-coloured, yellow, buds green. *Leaves* oblanceolate to lanceolate, 5–20 by 3–7.5 cm, apex acuminate, base cuneate, margins entire, hard chartaceous, lateral veins elevated above, 9–14 pairs, not glaucous, innovations light shining green above, adult leaves green, glaucous or not beneath; petiole red, 1.3–5 cm long, 0.6–1 mm wide. *Staminate inflorescences* 4–5.5 cm long, calyx caducous, stamens 8–10, anthers elliptic, apiculate, 1 mm long, 0.6 mm wide; pedicels 6–12 mm long. *Pistillate flowers* with bluish pruinose ovaries, stigmas bi-recurved, subsessile, purplish red, centre brown-black. *Fruiting axes* 3–4.5 cm long, 0.8 mm wide. *Drupes* oblique ovoid to ovoid-ellipsoidal, on a pendant axis, often numerous, green then dark brown, black, tuberculate or verrucose, 7–10 mm long, 7–9 mm wide; pedicels 6–8 mm long; fruit stalks 5–12 mm long. — **Fig. 3g.**

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Primary and secondary forest, at altitudes between 900 and 2660 m; frequently associated with *Castanopsis* or *Nothofagus*.

Notes — 1. The two varieties differ only by the surface of the drupes.

2. This species is similar to *Daphniphyllum glaucescens* and differs only by its caducous calyx.

12. *Daphniphyllum parvifolium* Quisumb. & Merr.

Daphniphyllum parvifolium Quisumb. & Merr., Philipp. J. Sc. 37 (1928) 161; T.C. Huang, Taiwania 12 (1966) 20, f. 40. — Type: *Ramos & Edaño 45708* (A holo; BM, NY, US).

Shrubs, 1–2 m high. *Leaves* small, fasciculate; blades narrowly oblong-obovate, apex rounded or mucronate, base cuneate, 4–9 by 1–2 cm, margins revolute, coriaceous, yellowish green above, brown and papillate beneath, lateral veins 6–9 pairs, impressed above, prominent beneath; petioles triangular, sulcate above, 7–25 cm long. *Staminate inflorescences* 1–2.5 cm long, flat, slightly flexuous, slender, 0.5 mm wide, calyx absent or 2-lobed, lobes short triangular, entire, free, stamens 5–10, filaments oblong, 0.4–0.6 mm long, 0.2 mm wide, anthers usually oblong to broadly elliptic, apiculate to obtuse at apex, 0.5–0.9 mm long, 0.3–0.5 mm wide, staminodia (called glands by Hayata) present, bracts broadly ovate, entire, longer than immature flowers, caducous; pedicels flat, 4–8 mm long, 0.2 mm wide. *Pistillate inflorescences* unknown. *Fruiting axes* terete, 2–6 cm long, 1 mm wide, calyx absent. *Drupes* oblong-ellipsoid, obtuse on both ends, 9–12 mm long, 4–5 mm in diam., smooth, obscurely wrinkled, black, styles divaricate or discoid, staminodia scars persistent; fruit stalk quadrangular, 3–7 mm long, 1 mm wide, bracts caducous. *Seed* elliptic globose, smooth, 8 mm long, 4 mm in diameter.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — Montane, on slopes and in mossy forest; 1800 m altitude.

Note — The species is characterized by its small, oblong-obovate leaves. It is similar to *D. buchananiifolium*, but differs by the narrower blades.

13. *Daphniphyllum scortechinii* Hook. f.

Daphniphyllum scortechinii Hook. f., Fl. Brit. India 5 (1887) 354. — *Daphniphyllum glaucescens* Blume subsp. *scortechinii* (Hook. f.) T. C. Huang, Taiwania 12 (1966) 195, f. 35. — Type: *Scortechini* s. n. (K holo; BM, BO, L).



Fig. 7. *Daphniphyllum scortechinii* Hook. f. a. Twig with fruits; b. ovary, longitudinal and cross sections; c. fruit, longitudinal section, and seed; d. staminate flower, stamen and anther in cross section (a: *Scortechini* s. n.; b: King's Coll. 1347; c: King's Coll. 830; d: Robinson s. n.).

Tiny tree, 2.5–6 m high. *Leaves* elliptic to obovate, apex mucronate, base obtuse, 5–6 by 3–4 cm, margins revolute, the reticulation very fine. *Staminate inflorescences* unknown. *Pistillate inflorescences* 2 cm long; flowers green in bud, calyx deeply 4- or 5-lobed, ovate, caducous, styles recurved, as long as ovary, pistillodes 1 or 2 in pistillate flowers; pedicels 4–6 mm long. *Fruiting axes* 3–6 cm long, 1 mm thick. *Drapes* ovoid, smooth, 7–8 mm long, 5–6 mm diam., green at youth, blue colour, without calyx; fruit stalks 5 mm long. — **Fig. 7.**

Distribution — *Malesia*: Peninsular Malaysia (Perak).

Habitat & Ecology — In stunted dense upper montane rain forest at altitudes of 1500 to 1900 m.

Note — The small and fine reticulation of this species can distinguish it from the closely related species *D. borneense*. The species differs from *D. neilgherrense* (Wight) K. Rosenthal by development of the style only; and from *D. gracile* by the latter's cuspidate apex of the leaves.

14. *Daphniphyllum sumatraense* (T.C. Huang) T.C. Huang

Daphniphyllum sumatraense (T.C. Huang) T.C. Huang, Blumea 41 (1996) 241. — *Daphniphyllum glaucescens* Blume subsp. *sumatraense* T.C. Huang, Taiwania 12 (1966) 166, f. 24. — Type: *Meijer 7199* (L. holo.; CANB).

Small tree, 2–4 m high, branchlets terete, canaliculate. *Leaves* alternate-fasciculate; blades lanceolate to narrowly elliptic, slightly falcate, apex acuminate, base cuneate, 5–10 by 2–4 cm, chartaceous, green above, glaucous and papillose beneath, veins 7–10 pairs, very thin, obscurely protruding on both surfaces, midrib slightly ascending beneath; petioles semi-terete, 1.5–2.5 cm long. *Staminate inflorescences* flat, 1.5–4.5 cm long, calyx shallowly campanulate, 4- or 5-lobed, lobes short, broadly triangular, acute at apex, margins entire or serrulate, c. 0.2 mm long, 0.4 mm wide; stamens 7–10, subsessile, filaments oblong, 0.1 mm long, apiculate or mucronate at apex, dorsally compressed; pedicels flat, 2–4 mm long. *Pistillate inflorescences* angulate, 2–4 cm long, calyx 4- to many-lobed, ovate or oblong, subentire, acute or irregularly divided at apex, c. 0.2 mm long, reticulate, caducous, ovary elliptic-globose, styles nearly as long as ovary, stigmas radiate-revolute; pedicels terete, 1–2 mm long. *Fruiting axes* angulate, 1.5–3.5 cm long. *Drapes* obliquely obovoid, acute at apex, 7 mm long, 4 mm in diam., black, tuberculate, staminodia present; fruit stalks 1–3 mm long.

Distribution — *Malesia*: Sumatra.

Habitat & Ecology — Secondary forests at altitudes from 500 to 1000 m.

Note — The species differs from *D. glaucescens* and *D. luzonense* by shorter fruiting pedicels, and from *D. lancifolium* by the small, smooth drupes.

15. *Daphniphyllum timorianum* (T.C. Huang) T.C. Huang

Daphniphyllum timorianum (T.C. Huang) T.C. Huang, Blumea 41 (1996) 242. — *Daphniphyllum glaucescens* Blume subsp. *timorianum* T.C. Huang, Taiwania 12 (1966) 192. — Type: *Schmutz 2982* (L. holo.).

Daphniphyllum gracile auct. non Gage: K. Rosenthal in Engl., Pflanzenr. 68 (IV. 147a) (1919) 1–16.

Small *tree*, 6–15 m tall, 5–20 cm diam., the outer bark smooth, light brown, 5 mm thick, living bark 3 mm thick, light brown. *Leaves* fascicled at tip of branchlets; blades elliptic, narrowly elliptic to oblong-elliptic, acute, acute-acuminate to cuspidate at apex, acute to obtuse at base, 5–15.5 by 2–4.5 cm, entire, green, thick-membranous, shining on both surfaces, lateral veins 6–8 pairs, veinlets reticulate, prominent on both surfaces; petioles 1.2–3 cm long, 1 mm thick. *Staminate inflorescences* racemes 2–3 cm long; male flowers reddish or pale green, calyx 4- or 5-lobed, triangular, persistent, stamens 5–10, anthers oblong, elliptic, 1–1.5 mm long, 0.8–1 mm thick, apiculate to cuspidate at apex; pedicels 3 mm long. *Pistillate inflorescences* 1–2 cm long, calyx of the female flower deeply 5-lobed, staminodes present, styles circinnate or divaricate, as long as or longer than ovary; pedicels 10–15 mm long. *Fruiting axes* 2–5 cm long. *Drupe*s ellipsoid, smooth to rugose, 8–12 mm long, 6–8 mm diam., calyx caducous on drupe, fruit stalks 0.5–1.8 cm long.

Distribution — *Malesia*: Lesser Sunda Islands (Flores, Timor).

Habitat & Ecology — Mountain areas at altitudes of 1100 to 1800 m.

Notes — 1. *Daphniphyllum* plants of higher elevations such as 1700–1800 m possess smaller oblong-elliptic blades and smooth drupes while those of lower elevations such as 1100–1675 m appear to have long oblong-elliptic blades and tuberculate drupes. All of them have thick membranous blades with more or less prominent reticulate venation on both surfaces.

2. This species is similar to *D. glaucescens* var. *blumeianum*, except for the somewhat longer shape of the blades.

16. *Daphniphyllum woodsonianum* T.C. Huang

Daphniphyllum woodsonianum T.C. Huang, Ann. Missouri Bot. Gard. 53 (1966) 28, f. 1; Taiwania 12 (1966) 199, f. 38. — Type: *van Steenis* 8362 (L holo).

Erect densely-leaved *shrub* or *tree*, c. 2 m high. *Leaves* verticillate or subverticillate; blades obovate, elliptic to narrowly elliptic, apex rounded, rarely emarginate to mucronulate, base obtuse, 4–7 by 2.5–4.5 cm, margins entire, coriaceous, thick-leathery, shining, smooth, brown on both surfaces, midrib whitish, lateral veins 7–9 pairs, thin, elevate-reticulate beneath; petioles broadly triangular, very short, thickened at the base. *Staminate inflorescences* oblong, 1.5–3 cm long, 0.2 mm wide, calyx absent or very shallowly cupuliform, stamens 8–11, filaments oblong, 1.3–2.3 mm long, anthers elliptic-ovate, 0.6–0.8 mm long with triangular apex 0.2 mm long; pedicels oblong, 4–7 mm long. *Pistillate inflorescences* angulate, 2.5–5 cm long; female flowers pale green, calyx oblong or obovate-oblong, subentire or with an irregularly divided apex, caducous, 0.4 mm long, 0.3 mm wide, ovary ovoid, stigma short, radiate or revolute; pedicels flat to terete, thickened toward apex, 2–3(–7) mm long. *Fruiting axes* 5 cm long. *Drupe*s ovoid-ellipsoid, 5–6(–8) mm long, 5 mm wide, blue-black, glaucous, fruit stalks c. 5 mm long. — **Fig. 8.**

Distribution — *Malesia*: Sumatra (Northern part).

Habitat & Ecology — Ridge forest, altitude 2500–3500 m.

Note — This species is similar to *D. scortechinii* except for the subsessile and subverticillate arrangement of the leaves and the absence of a calyx in the staminate flowers.



Fig. 8. *Daphniphyllum woodsonianum* T.C. Huang. a. Twig with pistillate inflorescence; b. part of pistillate inflorescence; c. ovary with longitudinal and cross sections; d. calyx; e. staminate inflorescence; f. naked staminate flower; g. stamen, dorsal and ventral views, and anther in cross section (van Steenis 8362).

ILLICIACEAE

(Richard M. K. Saunders, University of Hong Kong)¹

Illiciaceae A.C. Sm., *Sargentia* 7 (1947) 8, nom. cons.

One genus only.

ILLICIUM

Illicium L., *Syst. Nat.*, ed. 10 (1759) 1050; *Gen. Pl.*, ed. 6 (1764) 244; Ridl., *Fl. Malay Penins.* 1 (1922) 18; A.C. Sm., *Sargentia* 7 (1947) 10; Ng in *Tree Fl. Malaya* 2 (1973) 253; R.M.K. Saunders, *Bot. J. Linn. Soc.* 117 (1995) 341–342; in *Tree Fl. Sabah & Sarawak* 1 (1995) 227. — Type species: *Illicium anisatum* L.

Cymbostemon Spach, *Hist. Vég. Phan.* 7 (1839) 444. — Type species: *Cymbostemon parviflorus* Spach (syn. *Illicium parviflorum* Michx. ex Vent.).

Badianifera L. ex Kuntze, *Rev. Gen. Pl.* 1 (1891) 6. — Type species: *Badianifera anisata* Kuntze (syn. *Illicium anisatum* L.).

Shrubs or small to medium sized *trees*, evergreen, glabrous, aromatic with scattered ethereal oil cells. *Leaves* simple, entire, alternately arranged although often clustered to give appearance of whorls of 3–6 at distal nodes, exstipulate; lamina ovate to elliptic, papyraceous or coriaceous, pinnate venation, apex generally acuminate, base generally attenuate, decurrent; stomata on abaxial surface only, mesogenous, generally paracytic; petioles with groove on adaxial surface. *Flowers* solitary or in clusters of 2 or 3, mostly axillary, sometimes cauliflorous, bisexual, regular, hypogynous, 1–1.5 cm diam.; pedicels 0.5–7(–10) cm long. *Perianth* not differentiated into sepals and petals, segments numerous (7–33), free, overlapping at anthesis, spirally arranged, white, cream, pink, red or purplish. *Androecium* of (4–)numerous (up to c. 50) stamens, spirally arranged in one to several series; filaments short, thick; anthers basifixed, introrse to introrse-lateral, dehiscent by longitudinal slits; pollen grains binucleate, semitectate, tricolporate. *Gynoecium* of (5–)7–15(–21) free, conduplicate carpels, arranged in a single whorl, obliquely attached to receptacle; stigma dry, nonpapillate, decurrent; ovary unilocular, with single, near-basal, anatropous, bitegmic, crassinucellar ovule. *Fruit* a follicetum of single-seeded follicles, star-shaped, 2–3 cm across, green (ripening red), splitting along ventral edge of each segment when ripe. *Seeds* solitary in each segment, glossy, brown, with copious oily endosperm. — **Fig. 1.**

DISTRIBUTION

A medium sized genus, with a disjunct distribution in south-eastern North America, Mexico and the West Indies (5 species) and eastern Asia (centre of diversity, with about 35 species). The Asian distribution extends from southern Japan to the Malay Peninsula,

1) With contributions by R.W.J.M. van der Ham, Leiden (pollen morphology) and R. Hegnauer, Leiden (phytochemistry and chemotaxonomy). The drawing is by H.L. Wilks.

and from Assam to the Philippines. In *Malesia* 7 species: northern and central Sumatra, Malay Peninsula, Borneo (Sabah and Sarawak, with two records from Kalimantan), and the Philippines (Mindoro and Luzon).

HABITAT

The genus primarily occurs in subtropical evergreen forests, although some species extend into north temperate deciduous forests, and others (in Malesia) extend into tropical montane forests (c. 450 to 2000 m altitude).

ECOLOGY

Vegetative growth is markedly discontinuous, with periods of dormancy of vegetative buds alternating with active growth (Ng 1973). The resumption of growth involves the rapid elongation of buds to produce stems several centimetres long, which bear small caducous leaves; apical 'pseudowhorls' of leaves are then produced, consisting of alternately arranged normal leaves that are tightly clustered together.

Studies of the reproductive biology of the North American species *I. floridanum* Ellis and *I. parviflorum* Michx. ex Vent. have shown that they are pollinated by a wide variety of small insects, but primarily Diptera, with unspecialised feeding habits (Thien et al. 1983; White & Thien 1985). The plants typically grow in very dense populations and produce large numbers of flowers over a short period of time; the inefficiency of the insects in dispersing pollen, however, is suggested as one of the reasons for the typically low seed set. It has also been shown that a gametophytic self-incompatibility mechanism operates, and that the species frequently reproduce asexually by root suckers and runners (Thien et al. 1983; White & Thien 1985).

A system of ballistic seed dispersal (autochory) is apparent in *I. floridanum* (Roberts & Haynes 1983), although its efficacy in Malesian species has not been demonstrated. Seeds are expelled from the follicle as a result of hygroscopic tensions that develop in the succulent mesocarp walls and possibly also the sclerenchymatous endocarp. The role of water in the dispersal of seeds is unclear: whilst Thien et al. (1983) claim that the seeds can remain afloat for up to 10 days as a result of surface tension and the entrapment of air in an indentation of the testa at the point of attachment of the seed, Roberts & Haynes (1983) comment that mature seeds sink within 24 hours due to the absorption of water.

References: Ng, F.S.P. in Tree Flora of Malaya 2 (1973) 253–256. — Roberts, M.L. & R.R. Haynes, Pl. Syst. Evol. 143 (1983) 227–232. — Thien, L.B., et al., Amer. J. Bot. 70 (1983) 719–727. — White, D.A. & L.B. Thien, J. Elisha Mitchell Sci. Soc. 101 (1985) 15–18.

FOSSILS

The geographical occurrence of fossils of *Illicium* indicate that the genus previously had a comparatively wide distribution, occurring in Eocene to Pliocene boreotropical forests of Europe (e.g., Mai 1970a, b; Jähnichen 1976) and North America (e.g., Tiffney &

Barghoorn 1979), and in the Pliocene to Pleistocene of Japan (e.g., Miki & Kokawa 1962). Fossil evidence of the genus is comparatively rare, however, due in part to the susceptibility of the pollen to degradation, and most fossil remains are consequently of the distinctive coriaceous leaves (e.g., Jähnichen 1976). Other reports, however, describe the characteristic star-shaped fruits (e.g., Miki & Kokawa 1962; Mai 1970a, b; Tiffney & Barghoorn 1979). A progressive reduction in the number of floral parts can be inferred, despite the limited fossil material available (Tiffney & Barghoorn 1979).

Fossil pollen resembling *Illicium* pollen except that it is 6-colpate, was reported from the Cretaceous (Maastrichtian) of California (Chmura 1973). According to Thanikaimoni (1984) the fossil pollen genera *Terscissus* and *Trisectorius* from the Upper Cretaceous to Palaeocene of America (Tschudy 1970) cannot be attributed to the *Illiciaceae* because they lack the median ridges on the aperture membranes.

Gottwald (1992) described the fossil wood *Illicioxylon* from the Eocene of Germany as putatively affiliated to the *Illiciaceae*.

References: Chmura, C.A., *Palaeontographica* 141 (1973) 89–171. — Gottwald, H., *Palaeontographica* 225 (1992) 27–103. — Jähnichen, H., *Alttertiär. Abh. Zentr. Geol. Inst., Paläontol. Abh.* 26 (1976) 151–197. — Mai, D.H., *Paläontol. Abh., B, Paläobot.* 3 (1970a) 441–498; *Feddes Repert.* 81 (1970b) 347–370. — Miki, S. & S. Kokawa, *J. Biol., Osaka City Univ.* 13 (1962) 65–86. — Thanikaimoni, G., *Trav. Sect. Sci. Tech. Inst. Fr. Pondichéry* 18 (1984) 1–135. — Tiffney, B.H. & E.S. Barghoorn, *Amer. J. Bot.* 66 (1979) 321–329. — Tschudy, R.H., *U.S. Geol. Surv. Prof. Pap.* 643F (1970) 1–13.

ANATOMY

Leaf anatomy — The most comprehensive discussions of the leaf anatomy of *Illicium* are by Bailey & Nast (1948) and Metcalfe (1987). Characteristic features of the leaves include: conspicuously pitted abaxial epidermal cells, with undulating anticlinal walls and ridged cuticular thickenings; idioblastic sclereids in the mesophyll; and resin, ethereal oil and mucilage secretory cells in the mesophyll and occasionally also in the epidermis. The stomata are restricted to the abaxial leaf surface, and are paracytic (occasionally laterocytic), showing mesogenous development. The guard cells are dumb-bell-shaped, and often have large T-shaped cuticular thickenings at the stomatal poles (Baranova 1972). The leaf nodes are unilacunar, with a single vascular bundle.

Wood anatomy — The wood anatomy of the genus *Illicium* has been described in detail by Bailey & Nast (1948) and Carlquist (1982), including the Malesian species *I. ridleyanum* A.C. Sm. and *I. tenuifolium* (Ridl.) A.C. Sm. The genus has comparatively unspecialised wood, with a relatively uniform and stable secondary xylem. The vessel elements are almost exclusively solitary, and are long, thin-walled and polygonal, with scalariform perforation plates with numerous anastomosing bars; lateral pitting is scalariform to opposite. The fibre-tracheids bear conspicuous bordered pits. Axial parenchyma is sparse, abaxial to vessels with some diffuse cells also present. The rays are both uniseriate and narrowly multiseriate; the uniseriate rays consist of predominantly erect cells, although procumbent cells are found in some species.

References: Bailey, I.W. & C.G. Nast, *J. Arnold Arbor.* 29 (1948) 77–89. — Baranova, M., *Taxon* 21 (1972) 447–469. — Carlquist, S., *Amer. J. Bot.* 69 (1982) 1587–1598. — Metcalfe, C.R., *Anatomy of the Dicotyledons*, ed. 2, 3 (1987) 75–82.

FLORAL MORPHOLOGY

The floral structure in *Illicium* is primitive, with numerous spirally arranged organs around an elongated receptacle, and a regular perianth of unfused segments that do not form distinct sepals and petals [see discussions by Smith (1947) and Keng (1965, 1993)]. Although *Illicium* flowers tend to be comparatively uniform in structure, taxonomically significant variation is evident in several perianth characters, including tepal number, shape and colour. Keng (1965) has suggested that differences in tepal shape are correlated with the number of vascular bundles at the point of attachment to the receptacle: those with narrowly oblong, ligulate or lanceolate tepals possess a single main bundle at the base, whereas those with ovate to suborbicular tepals possess five or more basal bundles. Saunders (1995), however, has shown that all tepals in *Illicium* possess only a single basal vascular bundle, irrespective of their shape. The apparent distinction between the vascular patterns of the two tepal shapes is due to differences in the location of the dichotomous divisions of the vascular system: the bundle divides closer to the point of attachment in ovate to suborbicular tepals.

The number of stamens is also variable within the genus, and taxonomically valuable at the specific level. The filaments are short and thick, with a single broad vascular bundle, sometimes appearing as two separate bundles. The anthers have two lobes with two locules each, joined by a truncate connective, and show introrse or introrse-lateral dehiscence. The gynoecium consists of a whorl of free carpels that are attached laterally to the elongated receptacle; the number of carpels is also variable in the genus and taxonomically useful at the specific level.

Each carpel is differentiated into an enlarged ovary, short style and curved stigmatic crest with numerous papillae, and initially develops as a conduplicate structure (Robertson & Tucker 1979). Studies of mature floral structure, particularly with respect to the vasculature of filaments and carpels, indicate a putative reductive evolutionary trend in the genus (Keng 1965).

The floral ontogeny of several species has been described by Robertson & Tucker (1979), Erbar & Leins (1983), and Ronse Decraene & Smets (1993); the floral organs have been shown to develop in helical succession, with the carpels later appearing whorled.

References: Erbar, C. & P. Leins, *Bot. Jahrb. Syst.* 103 (1983) 433–449. — Keng, H., *Bot. Bull. Acad. Sin.* 6 (1965) 61–73; in: K. Kubitzki (ed.), *The families and genera of vascular plants*. Vol. 2: K. Kubitzki, J.G. Rohwer & V. Bittrich (eds.), *Flowering plants. Dicotyledons*. Berlin (1993) 344–347. — Robertson, R.E. & S.C. Tucker, *Amer. J. Bot.* 66 (1979) 605–617. — Ronse Decraene, L.P. & E.F. Smets, *Bot. J. Linn. Soc.* 113 (1993) 285–350. — Saunders, R.M.K., *Bot. J. Linn. Soc.* 117 (1995) 333–352. — Smith, A.C., *Sargentia* 7 (1947) 1–224.

1968; Okada 1975; Ratter & Milne 1976; Nagl et al. 1977), although the North American species *I. floridanum* has also been reported as $n = 13$ and $2n = 26$ (Stone 1965; Stone & Freeman 1968). The base number for the genus is therefore regarded as $x = 13$, 14. As this base number is also shared by the closely related family *Schisandraceae*, Ehrendorfer et al. (1968) have suggested that these two families (collectively forming the order *Illiciales*) diverged from the basic Magnolialean stock and extinct precursors with $x = 7$ by dysploid reduction from the palaeotetraploid level of $2x = 14$ to $2x = 13$.

References: Ehrendorfer, F., et al., *Taxon* 17 (1968) 337–353. — Morinaga, T., et al., *Bot. Mag. (Tokyo)* 43 (1929) 589. — Nagl, W., et al., *Pl. Syst. Evol.* 127 (1977) 103–105. — Okada, H., *J. Sci. Hiroshima Univ. ser. B (Bot.)*, 15 (1975) 115–200. — Ratter, J. A. & C. Milne, *Notes Roy. Bot. Gard., Edinb.* 32 (1973) 423–428; *ibid.* 35 (1976) 143–145. — Stone, D. E., *Madroño* 18 (1965) 122–126. — Stone, D. E. & J. L. Freeman, *J. Arnold Arbor.* 49 (1968) 41–51. — Whitaker, T. W., *J. Arnold Arbor.* 14 (1933) 376–385.

PHYTOCHEMISTRY AND CHEMOTAXONOMY

(R. Hegnauer)

Formerly *Kadsura*, *Illicium* and *Schisandra* were incorporated in *Magnoliaceae*. Later these three genera were united in a separate family called *Schisandraceae* s.l. (e.g. Gundersen 1950) or in two families, *Illiciaceae* (*Illicium* only) and *Schisandraceae* s.str. (*Kadsura* and *Schisandra*). Hegnauer (1973, 1990) treated chemical characters of all three genera sub *Schisandraceae* s.l.; many references and structural formulae are available in these two reviews.

Summarizing, the following statements seem to be adequate today.

The three fore-mentioned genera are well known in oriental medicine, especially in China, Korea, Taiwan and Japan. They have yielded a considerable number of crude drugs. A lot of chemical work has been performed in recent times with several of these medicinal plants. Nevertheless our knowledge of their chemical characters is still rather fragmentary. As far as chemical constituents are known they allow some preliminary taxonomic conclusions.

The production of essential oils and their deposition in idioblastic oil cells is shared by all three genera. This is a character of woody polycarps. There are marked differences, however, in secondary metabolism of *Kadsura* and *Schisandra* on the one side and *Illicium* on the other. The following special features of natural product chemistry are known from several taxa of the first mentioned two genera. 1) Production and accumulation of biologically active lignans belonging mainly to three types. The most peculiar lignans of *Kadsura* and *Schisandra* are bibenzocyclo-octadienoid compounds, such as the gomisins, the schizandrins and many others; they seem to be biogenetically related with bibenzylbutanoid-type lignans, e.g. anwulignan, pregomisin and others. 2) Moreover, both genera produce characteristic lanostane-type tetracyclic triterpenic acids. Striking structural features of some of these triterpenoids are a *seco*-A-ring and/or a rearranged C/D-ring-junction. However, very recently, similar triterpenoids were isolated from fresh twigs and leaves of *Illicium dunnianum* (Sy et al. 1997).

according to Fischer's law. Wodehouse (1935) already suggested that the colpi in *Illicium* and possibly the *Schisandraceae* may not be homologous with those of all other 3-colpate angiosperms. In a cladistic analysis of the *Magnoliidae* (Donoghue & Doyle 1989) the *Illiciaceae* proved to be the sister group of the *Schisandraceae*, and the *Winteraceae* the sister group of both families together. Doyle et al. (1990), using only pollen characters and adding several fossil pollen genera, and Loconte & Stevenson (1991), using pollen as well as macromorphological characters, found the same relationships and all three families appeared to be nested in a group possessing pollen with a single distal aperture. This implies that the colpi of *Illiciaceae* and *Schisandraceae* pollen are indeed not homologous with those of other 3-colpate angiosperms, but are independently derived from a single distal aperture such as present in modern *Winteraceae* (see also Liu & Yang 1989). In this view the heteropolar 3-colpate/syncolpate pollen of *Schisandra* p.p. and some collections of *I. anisatum* would be intermediate between the *Winteraceae* condition and the isopolar 3-(syn)colpate *Illicium* pollen. The presence of the three supplementary colpi that occur in the 6-aperturate *Schisandraceae* must be considered as a derived character. The above results would explain the exceptional orientation of colpi according to Garside's law in the *Illiciales*, because this is characteristic for the three arms of the distal aperture of trichotomosulcate angiosperm pollen (see also under *Schisandraceae*, page 187–189 in this issue).

References: Agababian, V.S., Biol. Zh. Armenii 19 (1966) 77–89. — Donoghue, M.J. & J.A. Doyle, Syst. Ass. Spec. Vol. 40A (1989) 17–45. — Doyle, J.A., C.L. Hutton & J.V. Ward, Amer. J. Bot. 77 (1990) 1558–1568. — Erdtman, G., Pollen morphology and plant taxonomy (1952). — Huang, T.C., Taiwania 13 (1967) 15–110; Pollen flora of Taiwan (1972). — Huynh, K.L., Beitr. Biol. Pflanzen 52 (1976) 227–253. — Ikuse, M., Pollen grains of Japan (1956). — Lieux, M.H., Pollen et Spores 22 (1980) 17–57. — Lin, Q., Bull. Bot. Res. 9 (1989) 115–124. — Liu, H. & C.S. Yang, Chin. J. Bot. 1 (1989) 104–115. — Loconte H. & D.W. Stevenson, Cladistics 7 (1991) 267–296. — Mitroiu, N., Acta Bot. Hort. Bucurest. 1969 (1970) 3–243. — Pokrovskaja, I.M., Ann. Serv. Inform. Géol. B.R.-G.G.M. 24 (1958) 1–435. — Praglowski, J., World Pollen Spore Flora 5 (1976) 1–32. — Saunders, R.M.K., Bot. J. Linn. Soc. 117 (1995) 333–352. — Takahashi, M., Grana 33 (1994) 309–312. — Walker, J.W., Linn. Soc. Symp. Ser. 1 (1976) 251–308. — Wodehouse, R.P., Pollen grains (1935).

SPOROGENESIS AND EMBRYOLOGY

Microsporogenesis (Hayashi 1960) and megasporogenesis and embryology (Hayashi 1963) have been described in detail for *Illicium anisatum*. The development of the embryo sac appears to conform to the *Polygonum* type, and the development of the embryo is of the Asterad type.

References: Hayashi, Y., Sci. Rep. Tôhoku Univ., ser. IV (Biol.), 26 (1960) 45–52; ibid. 29 (1963) 27–33.

CYTOLOGY

There is only one published chromosome count for a Malesian species of the genus *Illicium*: *I. stapfii* Merr. (syn. *I. cauliflorum* Merr.) is reported to have $n = 14$ and $2n = 28$ (Ratter & Milne 1973). The same number has been reported for four extra-Malesian species (Morinaga et al. 1929; Whitaker 1933; Stone & Freeman 1968; Ehrendorfer et al.

1968; Okada 1975; Ratter & Milne 1976; Nagl et al. 1977), although the North American species *I. floridanum* has also been reported as $n = 13$ and $2n = 26$ (Stone 1965; Stone & Freeman 1968). The base number for the genus is therefore regarded as $x = 13$, 14. As this base number is also shared by the closely related family *Schisandraceae*, Ehrendorfer et al. (1968) have suggested that these two families (collectively forming the order *Illiciales*) diverged from the basic Magnolialean stock and extinct precursors with $x = 7$ by dysploid reduction from the palaeotetraploid level of $2x = 14$ to $2x = 13$.

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Illicium contains several toxic species in Indochina, China, Korea, Taiwan, Japan, and the USA (*I. floridanum* ?; toxic constituents still unknown).

The toxins of *I. anisatum* L. (syn. *I. religiosum* Siebold & Zucc.) were investigated thoroughly and shown to be rearranged, dilactonic, picrotoxin-like sesquiterpenoids. Anisatin, neoanisatin and the non-toxic pseudoanisatin became first known from fruits (pericarps and seeds) of *I. anisatum* (Japanese Star Anise or Shikimi). Anisatin and pseudoanisatin are convulsants. Fruits of *I. anisatum* later yielded two other, but biogenetically related, types of C₁₅-dilactones, i.e. the majucin-type 6-deoxymajucin (Kouono et al. 1988) and the anislactone-type anislactones A and B (Kouono et al. 1990). Recently (Okuyama et al. 1993) trace amounts of anisatin-derivatives, i.e. veranisatin A and B, have been isolated from the spice Chinese Star Anise, which is derived from a cultigen of southern China and northern Vietnam that is known as *I. verum* Hook. f. The negligible amounts of these two new convulsants present in the fruits of *I. verum* are however without risk for their medicinal and culinary uses by man. Still another type of C₁₅-dilactones was detected in wood of *I. tashiroi*; two compounds were isolated and called illicinolide A and B (Fukuyama et al. 1992a). The same wood also yielded tashironin, C₂₂H₂₆O₆, which was shown to be the monobenzoate of a tricyclic rearranged sesquiterpenetriol; tashironin may be related to the C₁₅-progenitor of the *Illicium*-dilactones (Fukuyama et al. 1995). Toxic C₁₅-dilactones are presently known also from *I. dunnianum* Tutcher (Yang et al. 1988) and *I. majus* Hook. f. & Thomson.

The essential oils of fruits, leaves, barks, woods and other parts of *Illicium* taxa contain mainly phenylpropanoids, e.g. chavicol, eugenol, safrol and related propenyl- and allylbenzenoids, and mono- and sesquiterpenes. Their composition depends on taxa and plant parts. Anethol (= O-methylanol = *p*-methoxypropenyl-benzene) is the predominant oil constituent of Chinese Star Anise. Bark of *I. difengpi* B.N. Chang, a non-toxic Chinese taxon, also produces the rutinoside of 2-hydroxy-safrol and several derivatives of a dihydroconiferylalcohol 4-glycerinether (Kouono et al. 1992).

A tendency to prenylate phenylpropanoids in various ways is a special feature of *Illicium* taxa. O-Prenylation yields natural products like O-prenyleugenol and illicinol (= 2-prenyloxysafrol). C-Prenylation combined with reductions, rearrangements and cyclizations generates the so-called phytoquinoids, the illicinones and illifunones (Yakushijin et al. 1980, 1984). Wood of *I. tashiroi* Maxim. yielded many illicinones and illifunones. Illicinone E is one of its main constituents; it is accompanied by a whole array of derivatives, some of which are chlorinated (Fukuyama et al. 1992b, 1994).

In a number of *Illicium* taxa illicinones and illifunones seem to be replaced by lignane-like C₆-C₃-dimers and -trimers. Biphenyl-type neolignans (magnolol, honokiol) and triphenyl-type sesqueneolignans (dunnianol, macranthol, simonsinol) were isolated from Chinese material of *I. dunnianum*, *I. macranthum* A.C. Sm., *I. majus* and *I. simonsii* Maxim. (Kouono et al. 1994). Otherwise, *I. difengpi* and *I. majus* seem to produce predominantly neolignans of the aryldihydrobenzofuranpropanol-type. One of the neolignans of the bark of *I. difengpi* was shown to be identical with sakuraesinol, a glycerin ether already known from the bark of *Prunus jamasakura* Koidz. (Kouono et al. 1993).

Shikimic acid is one of the precursors of aromatic plant constituents. It was first isolated from fruits of *I. anisatum* (Shikimi) where it is present in large amounts and is accompanied by protocatechuic acid. Common plant phenolics such as hydroxybenzoic and hydroxycinnamic acids, flavonoids and proanthocyanidins seem to be ubiquitous in *Illicium*; however, their chemical investigation was rather neglected hitherto. Glycosides of the flavonols kaempferol and quercetin (isoquercitrin isolated from *Illicium* material) were detected in every investigated species including the American *I. floridanum* Ellis. The only recent investigations of common phenolics concern herbarium leaves of *I. manipurens* Watt ex King (Williams & Harvey 1982) and fresh bark of *I. anisatum* (Morimoto et al. 1988). The latter contains catechin, 6- and 8-prenylcatechin and much pro-cyanidins of which several dimeric and trimeric compounds were isolated.

The foregoing summary is based predominantly on investigations of Chinese, Taiwanese and Japanese (including the Ryukyus) plant material. Southern China, Taiwan and the Ryukyu Islands seem to be together the present centre of diversification of *Illicium* and the precise systematic status of many described taxa is still questionable. The following taxa are mentioned in recent phytochemical literature: *I. arborescens*, *I. difengpi*, *I. dunnianum*, *I. macranthum*, *I. majus*, *I. manipurens*, *I. religiosum*, *I. simonsii*, *I. tashiroi*, and *I. verum*.

The toxic dilactonic sesquiterpenes (anisatin, majucin, anislactones etc.), modified isoprenylated phenylpropanoids (illicinones, illifunones), prenylated catechins and bi-phenyl-type neolignans represent outstanding chemical features of *Illicium*. Such compounds have not yet been detected in *Kadsura* and *Schisandra*. Secondary metabolism, therefore, seems to agree with the treatment of *Illicium* as a separate family.

Johnson (1954) and Johnson & Fairbrothers (1965) have used serological techniques to verify the assertion by Smith (1947) that the genus does not have a close relationship with the *Magnoliales*.

References: Fukuyama, Y., et al., Tetrahedron 48 (1992a) 5847–5854; Phytochemistry 31 (1992b) 3975–3979; 36 (1994) 1497–1503; 37 (1994) 1653–1657; Tetrahedron Letters 36 (1995) 583–586. — Gundersen, A., Families of dicotyledons (1950). Chronica Botanica, Waltham, Mass. — Hegnauer, R., Chemotaxonomie der Pflanzen 6 (1973) 336–343, 745; 9 (1990) 520–527. — Johnson, M.A., Serol. Mus. Bull. 13 (1954) 1–5. — Johnson, M.A. & D.E. Fairbrothers, Bot. Gaz. 126 (1965) 260–269. — Kouono, I., et al., Chem. Pharm. Bull. 36 (1988) 2990–2992 (from seeds); 38 (1990) 3060–3063 (from pericarps); 40 (1992) 2461–2464; 42 (1994) 112–114. — Kouono, I., et al., Phytochemistry 32 (1993) 1573–1577. — Morimoto, S., et al., Phytochemistry 27 (1988) 907–910. — Okuyama, E., et al., Chem. Pharm. Bull. 41 (1993) 1670–1671. — Smith, A.C., Sargentia 7 (1947) 1–224. — Sy, L.-K., et al., Phytochemistry 44 (1997) 1099–1108. — Williams, C. & W.J. Harvey, Phytochemistry 21 (1982) 329–337; treats mainly *Winteraceae*; the flavonols kaempferol and quercetin and the flavanol dihydroquercetin, but no flavones detected in hydrolysed leaf extracts of *Illicium manipurens*; pro-cyanidins present. — Yakushijin, K., et al., Chem. Pharm. Bull. 28 (1980) 1951–1954; 32 (1984) 11–22. — Yang, C.-S., et al., Tetrahedron Letters 29 (1988) 1165–1168.

USES

The fruit of *Illicium verum* Hook. f. is the source of the spice Chinese Star Anise, used for flavouring food and liqueurs. Although this species does not occur in Malesia, the

spice has been imported extensively from China and is traded in Malaysia as 'bunga lawang' or 'adas china' (Burkill 1966). The fruits of the Japanese species *I. anisatum* (syn. *I. religiosum* Siebold & Zucc.) are poisonous, although small quantities can be used for flavouring, and are sometimes retailed in Southeast Asia; confusion with the Chinese Star Anise resulted in unsuccessful attempts to grow it in Singapore (Burkill 1966). There has been considerable confusion regarding the application of common names to *I. verum* and *I. anisatum* (Small 1996). Although the name 'star anise' is rather ambiguous, it is widely used commercially; its use for the poisonous species *I. anisatum* should therefore be avoided. Other *Illicium* species have various reported medicinal properties, often as a stomachics, carminatives, stimulants or vermifuges (Perry 1980). The timber is of very limited value due to the small size of the trees.

None of the Malesian species is of any reported ethnobotanical value.

References: Burkill, I.H., A dictionary of the economic products of the Malay Peninsula 2 (1966) 1244–1246. — Perry, L.M., Medicinal plants of East and Southeast Asia (1980) 180–181. — Small, E., Econ. Bot. 50 (1996) 337–339.

TAXONOMY

The taxonomic position of *Illicium* has been the source of considerable discussion, although its affinities with the *Magnoliales* have long been recognised; this is reflected historically by its classification in both the families *Magnoliaceae* (e.g., Bentham & Hooker 1862) and *Winteraceae* (e.g., Ridley 1922). The treatment that is most widely accepted today (proposed by Smith 1947), involves the isolation of *Illicium* in the monotypic family *Illiciaceae* on the basis of various morphological and anatomical criteria (discussed in detail by Bailey & Nast 1945, 1948). The *Illiciaceae* bear the closest relationship to the *Schisandraceae*, a small family of scrambling and twining woody vines. The isolated evolutionary position of these families has been recognised more recently by their classification as the sole members of the order *Illiciales* (e.g., Takhtajan 1980; Cronquist 1981); it is generally agreed, however, that the *Illiciales* were derived from a common ancestry with such orders as *Magnoliales* and *Winterales*, although the *Illiciales* are without very close modern relatives.

The last comprehensive revision of *Illicium* was the monograph by Smith (1947), who recognised 42 species. He divided the genus into two sections, viz. section *Badiana* Spach (which includes the type species and should therefore bear the autonym sect. *Illicium*), and section *Cymbostemon* (Spach) A.C. Sm. Section *Illicium* is characterised by narrowly oblong, ligulate or lanceolate inner perianth segments, and is represented in the Malesian flora by the distinctive species, *I. philippinense* Merr. The remaining six Malesian species belong to section *Cymbostemon*, which is characterised by generally ovate to suborbicular inner perianth segments. The two basic types of pollen in the genus (discussed above) are broadly correlated with the sectional distinctions, with trizonocolpate pollen occurring in sect. *Illicium* and trisyncolpate pollen in sect. *Cymbostemon*; although many of the Malesian species had not previously been studied palynologically, they are all shown by Saunders (1995) to conform to this taxonomic distinction.

The North American species *I. floridanum* (sect. *Illicium*) is atypical, however, since it possesses trisyncolpate grains (Wodehouse 1959; Lieux 1980).

References: Bailey, I.W. & C.G. Nast, J. Arnold Arbor. 26 (1945) 37–47; *ibid.* 29 (1948) 77–89. — Bentham, G. & J.D. Hooker, Genera Plantarum 1 (1862). — Cronquist, A., An integrated system of classification of flowering plants (1981). — Lieux, M.H., Pollen et Spores 22 (1980) 17–57. — Ridley, H.N., Flora of the Malay Peninsula 1 (1922). — Saunders, R.M.K., Bot. J. Linn. Soc. 117 (1995) 333–352. — Smith, A.C., Sargentia 7 (1947) 1–224. — Takhtajan, A., Bot. Rev. 46 (1980) 225–359. — Wodehouse, R.P., Pollen grains (1935, repr. 1959) 335–337.

KEY TO THE SPECIES

- 1a. Largest perianth parts narrowly elliptic (length: width ratio c. 2–4) **3. *I. philippinense***
- b. Largest perianth parts \pm ovate (length: width ratio c. 0.5–2) 2
- 2a. Leaves thin, papyraceous, becoming contorted along lateral veins after drying ... **7. *I. tenuifolium***
- b. Leaves thick, coriaceous, \pm flat after drying 3
- 3a. Leaves large, 5.5–14.5(–19) by 2–6.5(–8.5) cm; carpels 8–14; fruit of up to 14 follicles 4
- b. Leaves small, 3–9(–11.5) by 1.5–4(–5) cm; carpels 5–10; fruit of up to 10 follicles 6
- 4a. Stamens 9–19(–20); carpels 8–14 5
- b. Stamens 20–33(–39); carpels 12–13 **2. *I. peninsulare***
- 5a. Outermost perianth parts large, 4–8.5 by 4–6.5 mm; stamens 9–14(–20) **5. *I. stapfii***
- b. Outermost perianth parts small, 1.1–2.2 by 1.3–3 mm; stamens 15–19 **6. *I. sumatranum***
- 6a. Perianth parts 8–10(–13); stamens 7 or 8; carpels invariably 8; fruit of up to 8 follicles **1. *I. kinabaluense***
- b. Perianth parts 10–17; stamens (5–)9–19; carpels 5–10; fruit of up to 10 follicles **4. *I. ridleyanum***

1. *Illicium kinabaluense* A.C. Sm.

Illicium kinabaluense A.C. Sm., Sargentia 7 (1947) 61; R.M.K. Saunders, Bot. J. Linn. Soc. 117 (1995) 342; in Tree Fl. Sabah & Sarawak 1 (1995) 230. — Type: *Clemens 50154* (A holo; L), Mt Kinabalu, Sabah.

Small tree, to 14 m height, 90 cm girth. *Leaves* \pm coriaceous, elliptic, (4.5–)7(–11) by 1.5–3 cm, midrib \pm impressed above and prominent below, apex (short-)acuminate, base attenuate, margins slightly revolute; petioles c. 9–16 mm long, grooved on adaxial surface. *Flowers* axillary on young growth, generally solitary; pedicels 12–20 mm long at anthesis. *Perianth parts* 8–10(–13), pink, red or purplish, outermost perianth parts ovate, not reduced, 3.5–4.7–6 by 3–3.1–3.5 mm, largest perianth parts ovate, 4–5.4–7 by 2.5–3.4–5 mm, innermost perianth parts ovate, 2–3.6–5 by 1–1.8–2 mm. *An-*

androecium of 7 or 8 stamens, uniseriate; stamens 1.8–2.1–2.5 mm long; pollen grains trisyncolpate. *Gynoecium* of 8 carpels; carpels 1.6–1.8–2 mm long. *Fruit* of up to 8 follicles.

Distribution — *Malesia*: restricted to Mt Kinabalu, Sabah.

Habitat — Montane forests between 1200 and 2000 m altitude.

2. *Illicium peninsulare* A.C. Sm.

Illicium peninsulare A.C. Sm., Sargentia 7 (1947) 56; Keng in Fl. Thailand 2 (1972) 115; Ng in Tree Fl. Malaya 2 (1973) 254; R.M.K. Saunders, Bot. J. Linn. Soc. 117 (1995) 343. — Type: *Nur 11247* (A holo; UC), Fraser Hill, Pahang.

Illicium cambodianum auct. non Hance; King, J. As. Soc. Beng. 58, ii (1889) 374, pro parte.

Illicium cambodianum Hance var. *crassifolia* Ridl., Fl. Malay Penins. 1 (1922) 18, pro parte, nom. illeg.

Small tree, to 10 m height, 60 cm girth. *Leaves* coriaceous, elliptic, (9.5–)10–14.5 (–15) by 4–6.5 (–7) cm, midrib impressed above and very prominent below, apex acute to short acuminate, base attenuate, margins \pm revolute; petioles 11–20 mm long, grooved on adaxial surface. *Flowers* axillary on young growth, generally solitary; pedicels 1–7 (–10) mm long at anthesis. *Perianth parts* 15–25, yellowish white, outermost perianth parts broadly ovate, reduced, 2–2.9–3.5 by 2.8–3.5–4.8 mm, largest perianth parts ovate, 6.5–7.9–9.6 by 5–6.2–7 mm, innermost perianth parts ovate, c. 3.5 by 1.6 mm. *Androecium* of 20–33 (–39) stamens, biseriate; stamens 2.6–2.8–3 mm long; pollen grains trisyncolpate. *Gynoecium* of 12 or 13 carpels; carpels 3.2–3.7–4 mm long. *Fruit* of up to 13 follicles.

Distribution — Peninsular Thailand; *Malesia*: Malay Peninsula (Perak, Pahang, Selangor, Malacca, and Johore).

Habitat — Montane forests between 450 and 1520 m altitude.

Note — The *Illicium* species from the Malay Peninsula have been the source of considerable confusion due to their initial identification as *I. cambodianum*; this is discussed by Saunders (l.c.).

3. *Illicium philippinense* Merr.

Illicium philippinense Merr., Philipp. J. Sc., Bot. 4 (1909) 254; A.C. Sm., Sargentia 7 (1947) 33, f. 6H; H.L. Li in Fl. Taiwan 2 (1976) 405; R.M.K. Saunders, Bot. J. Linn. Soc. 117 (1995) 344. — Type: *Curran & Merritt 9515* (holo destroyed; US lecto; K), Luzon.

Illicium montanum Merr., Philipp. J. Sc., Bot. 7 (1912) 106. — Type: *Vanoverbergh 1048* (holo destroyed; K lecto), Luzon.

Shrub or small tree, to 8 m height. *Leaves* \pm coriaceous, elliptic, 5–7 (–9) by 2–4 cm, midrib \pm raised above and \pm prominent below, apex acute to acuminate, base attenuate, margins \pm revolute; petioles 8–10 mm long, groove \pm absent on adaxial surface. *Flowers* axillary on young growth, generally solitary or few in clusters; pedicels 5–15 mm long at anthesis. *Perianth parts* 15–27, white, outermost perianth parts ovate, c. 4.5 by 2.5–3 mm, largest perianth parts narrowly elliptic, 9–14 by 3.3–4.5 mm, innermost perianth parts ovate, c. 4.5 by 3 mm. *Androecium* of (11–)16–25 stamens, biseriate;

stamens 2.2–2.5–2.9 mm long; pollen grains trizonocolpate. *Gynoecium* of 9–11 carpels; carpels 3.3–3.7–4.5 mm long. *Fruit* of up to 11 follicles.

Distribution — Taiwan (Li, l.c.); *Malesia*: Philippines (Luzon, Mindoro).

Habitat — Montane forests between 800 and 3000 m altitude.

Note — The pollen has been illustrated by T.-C. Huang in Pollen Flora of Taiwan (1972) 125 and Saunders (l.c.).

4. *Illicium ridleyanum* A.C. Sm.

Illicium ridleyanum A.C. Sm., *Sargentia* 7 (1947) 66; Ng in *Tree Fl. Malaya* 2 (1973) 254; R.M.K. Saunders, *Bot. J. Linn. Soc.* 117 (1995) 344. — Type: *Robinson s.n.*, 18 Jan. 1913 (K holo), Selangor, Malay Peninsula.

Illicium cambodianum Hance var. *crassifolia* Ridl., *Fl. Malay Penins.* 1 (1922) 18, pro parte, nom. illeg.

Small *tree*, to 20 m height, 80(–120) cm girth. *Leaves* ± coriaceous, elliptic to ovate-elliptic, 3–9(–11.5) by (1.5–)2–4(–5) cm, midrib ± impressed above and very prominent below, apex acute or (short-)acuminate, base attenuate, margins ± revolute; petioles (5–)8–13 mm long, grooved on adaxial surface. *Flowers* axillary on young growth, generally solitary or few clustered; pedicels to c. 15 mm long at anthesis. *Perianth parts* 10–17, (pinkish-)red, outermost perianth parts broadly ovate, not reduced, 2–4.3–8 by 2.5–4–5.3 mm, largest perianth parts ovate, 4.1–6–8.4 by 4–5.7–8 mm, innermost perianth parts ovate, 1.3–2.9–5 by 0.6–1.5–2.5 mm. *Androecium* of (5–)9–19 stamens, uniseriate; stamens 0.8–2.2–3 mm long; pollen grains trisyncolpate. *Gynoecium* of 5–10 carpels; carpels 1.6–2.6–3.8 mm long. *Fruit* of up to 10 follicles.

Distribution — *Malesia*: Malay Peninsula (Perak, Kelantan, Trengganu, Pahang, Selangor, Malacca and Johore).

Habitat — Montane forests between 600 and 2040 m altitude.

Note — The *Illicium* species from the Malay Peninsula have been the source of considerable confusion due to their initial identification as *I. cambodianum*; this is discussed by Saunders (l.c.).

5. *Illicium stapfii* Merr.

Illicium stapfii Merr., *Philipp. J. Sc., Bot.* 13 (1918) 67; A.C. Sm., *Sargentia* 7 (1947) 65; R.M.K. Saunders, *Bot. J. Linn. Soc.* 117 (1995) 347; in *Tree Fl. Sabah & Sarawak* 1 (1995) 230. — Types: *Clemens 10995* (PNH lecto), *10949* (PNH para), *11081* (syn, destroyed), Mt Kinabalu, Sabah.

Illicium cauliflorum Merr., *Sarawak Mus. J.* 3 (1928) 522. — Type: *Mjöberg 114* (UC holo), Mt Murud, Sarawak.

Medium sized *tree*, to 25 m height, 80 cm girth. *Leaves* coriaceous, elliptic, (6–)10–14(–19) by 2–6(–8.5) cm, midrib markedly impressed above and prominent below, apex (short-)acuminate, acute or obtuse, base obtuse to attenuate, margins markedly revolute; petioles 10–35 mm long, groove on adaxial surface. *Flowers* axillary on young growth or occasionally ramiflorous/cauliflorous, generally solitary; pedicels up to 50 mm long at anthesis. *Perianth parts* 9–19, pink, red or purplish, outermost perianth

parts ovate, not reduced, 4–6.3–8.5 by 4–4.5–6.5 mm, largest perianth parts ovate, 5–7.4–9.5 by 3.4–5.1–7.6 mm, innermost perianth parts ovate 3.5–5.5–7.5 by 1–2.9–4.5 mm. *Androecium* of 9–14(–20) stamens, uniseriate; stamens 2–2.6–3.2 mm long; pollen grains trisyncolpate. *Gynoecium* of 8–14 carpels; carpels 2.1–3.1–5 mm long. *Fruit* of up to 14 follicles. $n = 14$, $2n = 28$ [Ratter & Milne, Notes Roy. Bot. Gard. Edinb. 32 (1973) 423–428].

Distribution — *Malesia*: Borneo, from Mt Kinabalu (Sabah) in the north to the Linau-Balui Plateau (Sarawak) in the south; also reported from northern Kalimantan.

Habitat — Montane forests between 800 and 2000 m altitude.

Note — The reduction of *I. cauliflorum* to a synonym of *I. stapfii* is discussed by Saunders (l.c.).

6. *Illicium sumatranum* A.C. Sm.

Illicium sumatranum A.C. Sm., Sargentia 7 (1947) 70; R.M.K. Saunders, Bot. J. Linn. Soc. 117 (1995) 347. — Type: *van Steenis 6317* (A holo; K), Aceh, Sumatra.

Small tree, to 15 m height. *Leaves* coriaceous, (narrow-)elliptic to slightly obovate, 5.5–13(–15) by 2–4.5(–5) cm, midrib very impressed above and very prominent below, apex acute to acuminate, base attenuate, margins highly revolute; petioles 5–13 mm long, grooved on adaxial surface. *Flowers* axillary on young growth, generally solitary; pedicels to c. 32 mm long at anthesis. *Perianth parts* 15–21, white to deep red (outer perianth parts often greenish), outermost perianth parts broadly ovate, reduced, 1.1–1.7–2.2 by 1.3–2.1–3 mm, largest perianth parts ovate, 4.7–5.7–7 by 3.5–4.9–6 mm, innermost perianth parts narrowly ovate, 2.4–3.3–4 by 1.6–1.8–2 mm. *Androecium* of 15–19 stamens, uni- or biseriate; stamens 1.6–2.3–2.9 mm long; pollen grains trisyncolpate. *Gynoecium* of 8–12 carpels; carpels 2.2–2.6–2.8 mm long. *Fruit* of up to 12 follicles.

Distribution — *Malesia*: Sumatra (Aceh, Sumatera Barat and Sumatera Utara).

Habitat — Montane forests between 1000 and 1800 m altitude.

7. *Illicium tenuifolium* (Ridl.) A.C. Sm.

Illicium tenuifolium (Ridl.) A.C. Sm., Sargentia 7 (1947) 68; Keng in Fl. Thailand 2 (1972) 116; Ng in Tree Fl. Malaya 2 (1973) 254, f. 1; R.M.K. Saunders, Bot. J. Linn. Soc. 117 (1995) 349. — *Illicium cambodianum* Hance var. *tenuifolia* Ridl., Fl. Malay Penins. 1 (1922) 18. — Type: *Ridley 13534* (K lecto), Pahang, Malay Peninsula.

Illicium cambodianum auct. non Hance: King, J. As. Soc. Beng. 58, ii (1889) 374, pro parte.

Illicium tenuifolium (Ridl.) A.C. Sm. var. *angustifolium* A.C. Sm., Sargentia 7 (1947) 70. — Type: *Robinson & Kloss 6089* (K holo), Kedah, Malay Peninsula.

Illicium tenuifolium (Ridl.) A.C. Sm. var. *obovatum* A.C. Sm., Sargentia 7 (1947) 70. — Type: *Sy- mington 24243* (K holo; SING), Selangor, Malay Peninsula.

Small tree, to 15 m height, 30 cm girth. *Leaves* papyraceous, becoming contorted after drying along secondary (and occasionally tertiary) veins, elliptic to obovate, (6.5–) 8–13(–19) by (2–)2.5–6 cm, midrib ± impressed above and ± prominent below, apex

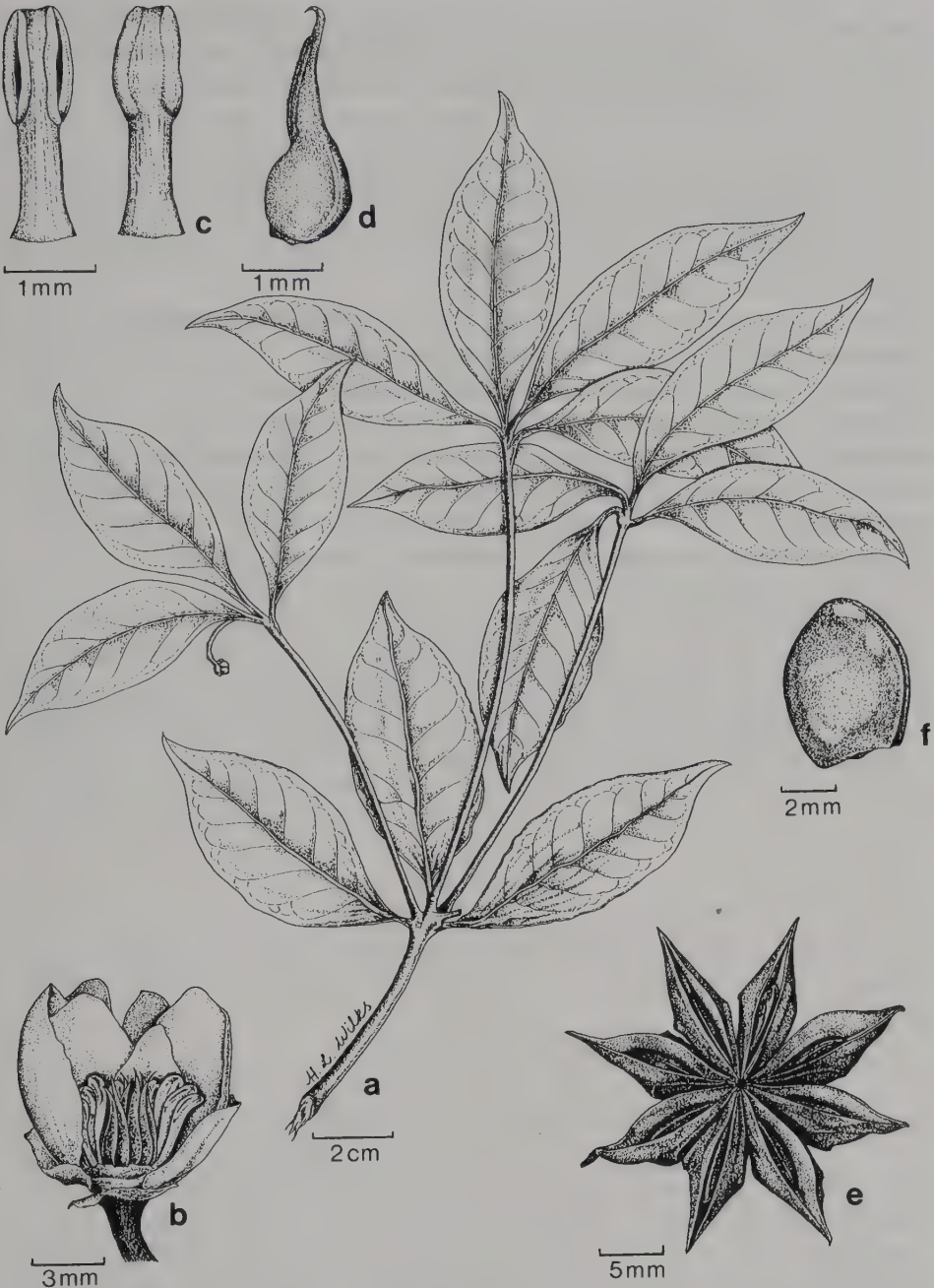


Fig. 1. *Illicium tenuifolium* (Ridl.) A.C. Sm. a. Flowering branch; b. flower, with proximal perianth parts and stamens removed; c. isolated stamens (abaxial and adaxial views); d. isolated carpel (lateral view); e. fruit (follicetum of eight follicles); f. seed (a: *H. & R. S. Keng* 4329; b: *de Wilde & de Wilde-Duyffes* 19036; c, d: *de Wilde & de Wilde-Duyffes* 13222; e: *Ding Hou* 810; f: *Ridley s.n.* Drawing by H.L. Wilks, reproduced with permission from Bot. J. Linn. Soc. 117 (1995).

(long-)acuminate, base attenuate, margins \pm revolute or not revolute; petioles 6–18 mm long, grooved on adaxial surface. *Flowers* axillary on young growth or ramiflorous/ cauliflorous, generally solitary or few clustered; pedicels 10–50 mm long at anthesis. *Perianth parts* 10–18, white to red, outermost perianth parts broadly ovate, reduced, 0.9–1.9–3.3 by 1–2–3.4 mm, largest perianth parts broadly ovate, 2.4–5.6–8.9 by 1.6–5.2–8.3 mm, innermost perianth parts ovate, 2.1–4.4–6.3 by 1.2–2.6–6.4 mm. *Androecium* of (8–)12–16(–20) stamens, uniseriate; stamens 1.7–2.7–3.8 mm long; pollen grains trisyncolpate. *Gynoecium* of (6–)8(–13) carpels; carpels 2.6–3.5–5.5 mm long. *Fruit* of up to 13 follicles. — **Fig. 1.**

Distribution — Peninsular Thailand; *Malesia*: Malay Peninsula (Kedah, Perak, Trengganu, Pahang, Selangor, Negri Sembilan and Johore).

Habitat — Montane forests between 420 and 1680 m altitude.

Notes — 1. The *Illicium* species from the Malay Peninsula have been the source of considerable confusion due to their initial identification as *I. cambodianum*. This is discussed by Saunders (l.c.), as is the validity of the infraspecific classification proposed by Smith (l.c.).

2. The pollen of the present species is illustrated by Saunders (l.c.).

EXCLUDED

Illicium evenium King, J. As. Soc. Beng. 58, ii (1889) 374–375 = *Ternstroemia evenia* (King) A.C. Sm., Sargentia 7 (1947) 78 (*Theaceae*) [syn. *Ternstroemia scortechinii* King, J. As. Soc. Beng. 59, ii (1890) 193].

SCHISANDRACEAE

(Richard M. K. Saunders, University of Hong Kong)¹

Schisandraceae Blume, Fl. Javae 32–33 (1830) 3, '*Schisandreae*', nom. cons.; G. Don, Gen. Hist. 1 (1831) 101, '*Schizandriaceae*'; Ridl., Fl. Malay Penins. 1 (1922) 20, '*Schizandraceae*'; A. C. Sm., Sargentia 7 (1947) 81–83; Backer & Bakh. f., Fl. Java 1 (1964) 98.

Woody vines, monoecious or dioecious. *Leaves* alternate or \pm clustered, exstipulate, petiolate; lamina simple. *Flowers* generally solitary and axillary to leaves on ultimate branches, or in axils of fugacious bracts near base of ultimate shoots, occasionally in pairs or in clusters of up to 8, unisexual, hypogynous, few to numerous parts generally spirally arranged, pedicellate. *Perianth segments* free, not as distinct sepals and petals, outermost and innermost sometimes reduced. *Androecium* very variable, of few to many (4–80) stamens, sometimes of \pm free stamens fused only at base of filaments, sometimes as head of fused stamens or free but tightly compressed stamens; anthers essentially basifixed, thecae dehiscent by longitudinal slits; filaments at least basally fused into modified column of variable shape. *Gynoecium* of numerous (12–300) carpels; carpels developmentally conduplicate; stigmatic crest as subulate to broad essentially unvascularised 'pseudostyle', sometimes modified as peltate or irregular 'pseudostigma'; ovary unilocular; ovules 2–5(–11), anatropous, ventrally attached or pendulous, bitegmic, crassinucellar. *Fruit* an aggregate of berries; receptacle ellipsoid to elongate; berries with fleshy pericarp. *Seeds* 1–5, rarely more, ventrally attached or pendulous, laterally flattened, with copious oily endosperm.

DISTRIBUTION

The *Schisandraceae* have a disjunct distribution, occurring in Asia (c. 46 species, with a centre of diversity in continental Asia) and in south-eastern North America (1 species).

HABITAT AND ECOLOGY

The *Schisandraceae* are scrambling or twining woody vines of tropical to warm temperate (rarely cool temperate) forests.

Ueda (1988) has studied the occurrence of dioecy in *Schisandra chinensis* (Turcz.) Baill. Although this species is monoecious, it often appears to be dioecious, and has the capability to change sex expression over several years of growth; similar results are reported in *Kadsura japonica* (L.) Dunal by Okada (1971). Smith (1947) described 19 of

1) With a contribution by R.W.J.M. van der Ham, Leiden (pollen morphology). Drawings by H.L. Wilks.

the total 25 accepted species of *Schisandra* as dioecious; it is probable, however, that most if not all *Schisandraceae* species are monoecious, with many showing temporal separation of male and female flowers.

References: Okada, H., J. Jap. Bot. 46 (1971) 29–33. — Smith, A. C., Sargentia 7 (1947) 1–224. — Ueda, K., J. Jap. Bot. 63 (1988) 319–321.

FOSSILS

The geographical occurrence of fossils of the *Schisandraceae* indicates that the family previously possessed a wider distribution, with records from the Eocene of Europe (e.g., Mai & Walther 1985) and North America (e.g., Bones 1979), and the Pliocene of Japan (e.g., Tanai 1976). The records suggest a Laurasian origin for the family, with extension into the New World developing later.

Fossil pollen attributed to *Schisandra* is known from the Miocene of Borneo, and *Schisandra* section *Pleiostema* (pollen type A of Pragłowski 1976) from the Upper Cretaceous (Maastrichtian) of California (Muller 1970; Chmura 1973)).

References: Bones, T. J., Oregon Mus. Ser. Industr. Occas. Pap. 1 (1979) 1–23. — Chmura, C. A., Palaeontographica 141 (1973) 89–171. — Mai, D. H. & H. Walther, Abh. Staatl. Mus. Mineral. Geol. Dresden 33 (1985) 1–260. — Muller, J., Biol. Review 45 (1970) 417–450. — Pragłowski, J., World Pollen Spore Flora 5 (1976) 1–32. — Tanai, T., J. Fac. Sci. Hokkaido Univ. IV, 17 (1976) 277–346.

VEGETATIVE ANATOMY

The most comprehensive discussions of the vegetative structure of the family are by Bailey & Nast (1948) and Metcalfe (1987).

The leaves of the *Schisandraceae* frequently show marginal denticulation, although this is variable. Characteristic features of the leaf anatomy include: epidermal cells with undulating or sinuous anticlinal walls; and mixed paracytic and laterocytic stomata (Baranova 1983), with cuticular intrusions between the ends of the two members of each pair of guard cells (but with smaller intrusions than observed in the closely related family *Illiciaceae*). The nodes are unilacunar, with three leaf traces.

The internodal regions of the stem have either a eustelic or a siphonostelic vascular arrangement. The secondary xylem (Bailey & Nast 1948; Metcalfe 1987) is also variable, ranging from a relatively primitive dense to specialised highly porous arrangement. The more primitive type is characterised by narrow vessel members with scalariform perforation plates; thick-walled tracheids; multiseriate rays with intervening high-celled uniseriate rays; and scanty diffuse and abaxial paratracheal wood parenchyma. The more advanced type is characterised by broad vessel members with a single large lacuna; large, thin-walled profusely pitted tracheids; mostly uniseriate rays; and abundant paratracheal wood parenchyma. The phloem contains numerous elongated or cambiform elements with stratified mucilaginous contents. The sclerenchyma is linear, elongated and fibre-like.

References: Bailey, I. W. & C. G. Nast, J. Arnold Arbor. 29 (1948) 77–89. — Baranova, M., Brittonia 35 (1983) 93–102. — Metcalfe, C. R., Anatomy of the Dicotyledons, ed. 2, 3 (1987) 83–89.

FLORAL MORPHOLOGY

Inflorescence structure is discussed in detail by Weberling (1988). Many species produce solitary flowers from the leaf axils, on branches which bear numerous scale-like leaves (presumably acting as bud scales) at the base of the axis. Other species produce flowers in the axils of fugaceous bracts; the two lowermost bracts (prophylls) bear vigorous buds that enable continued growth. Transitional forms also occur.

The flowers of the *Schisandraceae* are relatively primitive structurally as in the *Illiciaceae*, with spirally arranged floral organs and perianth segments that do not form distinct sepals and petals. A major distinction between the *Illiciaceae* and the *Schisandraceae*, however, is that the latter family is monoecious (although possibly dioecious in some species), whereas the *Illiciaceae* possess hermaphrodite flowers.

The female flowers of the *Schisandraceae* are structurally primitive, with numerous (12–300) free conduplicate carpels spirally arranged around the receptacle, with stigmatic crests that lack a distinct style (although sometimes with an essentially unvascularised 'pseudostyle'). The two genera in the family are largely distinguished on the basis of the shape of the receptacle in the female flower (and consequently the shape of the aggregate fruit) and the structure of the stigmatic crest; the taxonomic significance of this is discussed further below.

The male flowers show great variation in androecial anatomy, although this cannot be used taxonomically at the generic level. The more primitive species in both genera in the family possess numerous stamens that are united by fusion of the base of the filaments. Many of the more advanced members of the family show an evolutionary change that is superficially parallel, with aggregation of stamens in compact (sub)globose heads; a distinction can be made between the two genera, however, as the stamens are either fused together to form a carnosse mass, or else are tightly compressed but free. Other members of the family show an evolutionary reduction in the number of stamens, with as few as four in one species. The variation in the androecial structure is discussed in greater detail under the generic treatments.

Reference: Weberling, F., *Taxon* 37 (1988) 657–690.

POLLEN MORPHOLOGY

(R.W.J.M. van der Ham)

Pollen of both *Kadsura* and *Schisandra*, showing a suite of remarkable features, has been given much attention in the palynological literature (e.g., Wodehouse 1935, 1936; Erdtman 1952; Jalan & Kapil 1964; Agababian 1966; Mitroiu 1970; Walker 1974; Huynh 1976; Lieux 1980). The most extensive study, illustrated with light and electron micrographs, is by Praglowski (1976) and treats more than half of all species, including seven Malesian *Kadsura* species and one Malesian *Schisandra*.

Schisandraceae pollen grains are heteropolar 3- or 6-aperturate monads. Grain size is 22–35 μm . Grain shape is usually oblate ($P/E = 0.44\text{--}0.78$); the proximal pole is less convex than the distal pole. The equatorial outline is rounded to obtusely triangular or hexagonal. The aperture system is 3-demisynecolpate, the colpi being connected at the

distal pole, either with or without three free short colpi alternating with them. Huynh (1976) demonstrated that the long colpi are arranged according to Garside's law, and the short colpi according to Fischer's law. Deviating systems like the parasyncolpate and trischistoclastic type occasionally occur. All colpi are mostly provided with thickened edges and a broadly based median ridge (Roland 1971), which may act as a rigid frame (Wodehouse 1935; Pragłowski 1976). There are no endoapertures. Germination takes place by dehiscence of the syncolpate apertures, starting at the pole, followed by extrusion of the pollen grain contents and then by pollen tube formation (Huynh 1976). The short colpi are not involved in germination or harmomegathy; the relatively thin-walled proximal apocolpium seems to accommodate the volume changes of the pollen grain. The exine is up to 2.5 μm at the distal pole, up to 1.5 μm at the proximal pole, and clearly stratified, showing a thin nexine and thick sexine, which consists of a columellate infratectum and a reticulate tectum with lumina of 2–8 μm . The nexine includes a distinct endexinous layer, which is differentiated under the colpi into a lamellate outer and a spongy inner sublayer.

Pragłowski (1976) distinguished four pollen types in the *Schisandraceae*: type A is 3-aperturate, while types B, C, and D are 6-aperturate, differing only in the size of the lumina. Type A is restricted to a few species of the primitive *Schisandra* section *Pleio-stema*, which all have a large number (20–60) of essentially free stamens, and therefore appears to be the plesiomorphic type. Type D, which possesses the largest lumina (6–8 μm), is found only in *Schisandra chinensis*. Types B and C occur in both *Kadsura* and *Schisandra*, which implies that these genera cannot be separated palynologically. Pollen of the *Schisandraceae*, especially the 3-aperturate type, resembles *Illicium* pollen very much; except for very rare intermediate forms, the latter can be distinguished by its isopolar aperture system (see *Illiciaceae*, this issue, p. 173–174). Walker & Doyle (1975) and Thanikaimoni (1984) noted the similarity of *Schisandra* pollen and that of the menispermaceous genus *Tinospora*.

Wodehouse (1935, 1936; see also Jonker 1974), assuming the syncolpate pole to be the proximal one, considered 6-aperturate *Schisandraceae* pollen as a combination of features of pteridophyte spores (proximal trichotomous aperture with arms arranged according to Garside's law), gymnosperm and monocot pollen (thin distal area) and dicot pollen (three meridional colpi arranged according to Fischer's law), thus being a curious link between spores and the basic dicot pollen type. Erdtman (1952) and Muller (1970) proposed that the syncolpate pole has a distal orientation. Later, Huynh (1976) and Pragłowski (1976) observed tetrad configurations which actually demonstrated the syncolpate pole to be at the distal side. It is now hypothesised that *Schisandraceae* and *Illiciaceae* pollen was derived from a type with a single distal aperture and united in tetrads, as in modern *Winteraceae* (see also *Illiciaceae*, this issue, p. 173–174). Then, the relatively thin-walled proximal apocolpium in *Schisandraceae* pollen might be a vestige of an ancestral tetrad configuration, as in most adult tetrads proximal walls are reduced (Doyle et al. 1990). At the same time the above hypothesis entails the independent origin of the three short colpi in *Schisandraceae* pollen and those in the basic dicot pollen type.

Fossil pollen is mentioned above, under Fossils.

References: Agababian, V.S., Biol. Zh. Armenii 19 (1966) 77–89. — Doyle, J.A., C.L. Hutton & J.V. Ward, Amer. J. Bot. 77 (1990) 1558–1568. — Erdtman, G., Pollen morphology and plant taxonomy (1952). — Huynh, K.L., Beitr. Biol. Pflanzen 52 (1976) 227–253. — Jalan, S. & R.N. Kapil, Grana Palynol. 5 (1964) 216–221. — Jonker, F.P., Adv. Pollen-Spore Res. 1 (1974) 50–61. — Lieux, M.H., Pollen et Spores 22 (1980) 17–57. — Mitroiu, N., Acta Bot. Hort. Bucurest. 1969 (1970) 3–243. — Muller, J., Biol. Rev. 45 (1970) 417–450. — Praglowski, J., World Pollen Spore Flora 5 (1976) 1–32. — Roland, F., Rev. Gén. Bot. 78 (1971) 329–338. — Thanikaimoni, G., Trav. Sect. Sci. Tech. Inst. Fr. Pondichéry 18 (1984) 1–135. — Walker, J.W., Amer. J. Bot. 61 (1974) 1112–1137. — Walker, J.W. & J.A. Doyle, Ann. Missouri Bot. Gard. 62 (1975) 664–723. — Wodehouse, R.P., Pollen grains (1935); Bot. Rev. 2 (1936) 67–84.

SPOROGENESIS AND EMBRYOLOGY

Microsporogenesis (Hayashi 1960; Kapil & Jalan 1964; Vijayaraghavan & Dhar 1975), megasporogenesis and embryology (Yoshida 1962; Hayashi 1963; Kapil & Jalan 1964; Swamy 1964; Davis 1966) have been studied in detail for several species of *Schisandra* and *Kadsura*. The tapetum is glandular and binucleate, pollen mother cell divisions are simultaneous and the pollen grains are 2-celled when the anther dehisces. The development of the embryo sac appears to be of the *Polygonum* type, and the development of the embryo is of the Asterad or Onagrad type.

References: Davis, G.L., Systematic embryology of Angiosperms (1966). — Hayashi, Y., Sci. Rep. Tôhoku Univ., IV (Biol.), 26 (1960) 45–52; 29 (1963) 403–411. — Kapil, R.N. & S. Jalan, Bot. Not. 117 (1964) 285–306. — Swamy, B.G.L., J. Ind. Bot. Soc. 43 (1964) 391–396. — Vijayaraghavan, M.R. & U. Dhar, J. Arnold Arbor. 56 (1975) 176–182. — Yoshida, O., J. Coll. Arts Sci. Chiba Univ. 3 (1962) 459–462.

CYTOLOGY

The base chromosome number of the family is regarded as $x = 7, 13$. As this base number is also shared by the closely related family *Illiciaceae*, Ehrendorfer et al. (1968) have suggested that these two families (collectively forming the order *Illiciales*) diverged from the basic Magnolialean stock and extinct precursors with $x = 7$ by dysploid reduction from the palaeotetraploid level of $2x = 14$ to $2x = 13$.

Reference: Ehrendorfer, F., et al., Taxon 17 (1968) 337–353.

PHYTOCHEMISTRY AND CHEMOTAXONOMY

See the relevant chapter in the treatment of *Illiciaceae* (this issue, p. 175).

USES

The uses of both *Kadsura* and *Schisandra* are discussed under these genera.

TAXONOMY

The most recent comprehensive taxonomic revision of the family is by A.C. Smith (1947, cited earlier), who accepted two genera, *Schisandra* with 25 species and *Kad-*

sura with 22 species. The distinction between the two genera is largely based on gynoeceal and fruit characters. *Kadsura* is characterised by female flowers with obovoid, subclavate or ellipsoid receptacles that are only slightly longer than wide, and which remain comparatively short after fertilisation; the aggregate fruits are consequently subglobose clusters of berries. In marked contrast, *Schisandra* is characterised by female flowers with cylindrical or conical receptacles that are markedly longer than wide, and which become highly elongated in the fruits. Differences also exist in relation to the stigmas, which are broad and often peltate in *Kadsura*, but narrow and subulate in *Schisandra*. The generic distinctions are not reflected in androecial structure, however, which makes the identification of specimens that bear only male flowers problematic. This difficulty is particularly acute with regard to species belonging to the more primitive sections *Cosbaea* of *Kadsura* and *Pleioestema* of *Schisandra*, which tend towards the hypothetical ancestral type. This problem is obviated within Malesia, however, as none of the *Kadsura* species described in the region belong to sect. *Cosbaea*.

KEY TO THE GENERA

(applicable to Malesian taxa only)

- 1a. Androecium subglobose, composed of tightly compressed but free stamens (superficially appearing connate). Pseudostyle either subulate or enlarged distally to form subpeltate pseudostigma. Fruits aggregated in capitate head, without extension of the receptacle after fertilisation **Kadsura** (p. 190)
- b. Androecium *either* subglobose, composed of connate stamens, forming androecial mass with sessile anthers, *or* androecium composed of stamens with essentially free filaments, \pm fused at base. Pseudostyle invariably subulate, without pseudostigma. Fruits borne on elongate axis, following extension of the receptacle after fertilisation **Schisandra** (p. 202)

KADSURA

- Kadsura* Kaempf. ex Juss., Ann. Mus. Hist. Nat. 16 (1810) 340; Ridl., Fl. Malay Penins. 1 (1922) 20; A.C. Sm., Sargentia 7 (1947) 156; Backer & Bakh. f., Fl. Java 1 (1964) 99; Saunders, Gard. Bull. Sing. (in press). — Type species: *Kadsura japonica* (L.) Dunal.
- Sarcocarpon* Blume, Bijdr. (1825) 21. — *Sarcocarpon* Blume ex G. Don, Gen. Hist. 1 (1831) 101. — Type species: *Sarcocarpon scandens* Blume [= *Kadsura scandens* (Blume) Blume].
- Panslowia* Wight ex Arn., Mag. Zool. Bot. 2 (1838) 546, pro syn.
- Pulcheria* Noroña ex Hassk., Cat. Pl. Hort. Bot. Bog. (1844) 177, pro syn.; Noroña, Verh. Batav. Gen. 5 (1790) art. 5: 3, nom. nud.
- Cosbaea* Lem., Ill. Hort. 2 (1855) 71. — Type species: *Cosbaea coccinea* Lem. [= *Kadsura coccinea* (Lem.) A.C. Sm.].
- Schizandra* sect. *Kadsura* Baill., Hist. Pl. 1 (1868/69) 189. — Type species: *Kadsura japonica* (L.) Dunal.

Woody lianes, monoecious. *Leaves* alternate, exstipulate; lamina papyraceous to coriaceous, elliptic to ovate, apex acute or acuminate, base cuneate (especially when young),

obtuse, truncate or subcordate, margins denticulate to entire, venation pinnate, brochidodromous; petioles with groove on adaxial surface. *Flowers* unisexual, in axils of leaves or fugaceous bracts, generally solitary, occasionally with secondary flower growing in axil of prophyll, or in clusters of 2–4 growing from glomerules, occasionally cauliflorous. *Perianth segments* 7–24, imbricate at anthesis, outermost and innermost segments \pm reduced, suborbicular, elliptic or ovate, rarely obovate, white, cream, yellow, pink or red, outer segments often green. *Androecium* of numerous (13–80) stamens; stamens sometimes \pm free but connate at base of filaments and occasionally with several subulate appendages attached to distal apex of receptacle, stamens sometimes aggregated into subglobose head with connectives either broader than thick with thecae of adjacent stamens contiguous, or else with connective as broad as thick with thecae of adjacent stamens not contiguous; pollen grains hexacolpate, distally syncolpate. *Gynoecium* of numerous (17–c. 300) carpels; receptacle obovoid or subclavate or ellipsoid, only slightly longer than broad; stigmatic crest forming subulate or laterally flattened ‘pseudostyle’, or modified as subpeltate or irregular ‘pseudostigma’; ovary with 2–5(–11) pendulous or ventrally attached ovules. *Fruit* a subglobose aggregate of berries attached to ellipsoid or clavate receptacle; berries subglobose to obovoid or elongate-obovoid, ripening red or yellow; peduncle often enlarged in fruit. *Seeds* 1–5, smooth, hilum lateral or apical. — **Fig. 1.**

Distribution — There are about 22 species in the genus, with a southern Chinese and Indo-Chinese centre of distribution, extending from southern Japan in the north-east to Sulawesi and Java in the south-east, and eastern India and Sri Lanka in the west. See A.C. Smith, *Sargentia* 7 (1947) 1–224. In *Malesia* 9 species, from Sumatra and peninsular Malaysia extending to the Philippines and east as far as Ceram, although absent from the Lesser Sunda Islands with the exception of Bali.

Habitat & Ecology — As for the family.

Floral morphology — The female flowers of *Kadsura* are characterised by receptacles that are obovoid, subclavate or ellipsoid (only slightly longer than wide) which do not become greatly elongated in the fruit, and by carpels with ‘pseudostyles’ that are either subulate or else expanded to form a subpeltate ‘pseudostigma’. Although the difference in stigmatic crest structure is generally species specific, *K. lanceolata* King is highly variable. The great variation evident in the structure of the androecium was used by Smith (1947) as the basis of his sectional classification of the genus (discussed below). The most primitive androecial type in the genus consists of numerous essentially free stamens that are only fused by the base of the filaments. According to Smith (1947), three distinct evolutionary trends are evident: 1) development of several subulate appendages on the distal apex of the receptacle; 2) aggregation of the stamens to form a subglobose head in which the individual stamens bear their thecae dorso-laterally, so that the thecae of adjacent stamens are not in contact; and 3) a similar aggregation to the above, but with the thecae borne laterally and consequently in contact with the thecae of adjacent stamens.

Reference: Smith, A.C., *Sargentia* 7 (1947) 1–224.

Cytology — Only two species of *Kadsura*, *K. japonica* (L.) Dunal and *K. longipedunculata* Finet & Gagnep., have been examined cytologically. Both are reported to have $2n = 28$ (Whitaker 1933; Okada 1971, 1975; Chen et al. 1993; Wu & Huang 1995). The generic base number is therefore taken to be $x = 14$.

References: Chen, R.-Y., et al., Chromosome Atlas of Chinese Principal Economic Plants 1 (1993) 321–322. — Okada, H., J. Jap. Bot. 46 (1971) 29–33; J. Sci. Hiroshima Univ. B (Bot.) 15 (1975) 115–200. — Whitaker, T.W., J. Arnold Arbor. 14 (1933) 376–385. — Wu, Z. & C. Huang, Guihaia 15 (1995) 47–51.

Uses — *Kadsura* is of little economic value, although *K. scandens* (Blume) Blume is used for various medicinal purposes and produces edible fruits (discussed under the species, below).

Taxonomy — The most comprehensive taxonomic revision of the genus is by A.C. Smith (1947), who accepted 22 species. As with *Schisandra*, Smith recognised several sections in *Kadsura* on the basis of differing androecial structure: 1) sect. *Cosbaea* (Lem.) A.C. Sm., in which the stamens are aggregated into a conical structure, sometimes surmounted by numerous subulate appendages; 2) sect. *Sarcocarpon* (Blume) A.C. Sm., in which the androecium is subclavate, with essentially sessile anthers closely appressed in a subglobose or ellipsoid head, and connectives that are as broad as thick, so that the thecae of adjacent stamens are not contiguous; and 3) sect. *Kadsura* (as '*Eukadsura*'), which is essentially the same as sect. *Sarcocarpon*, except that the connectives are considerably broader than they are thick, so that the thecae of adjacent stamens are contiguous. Section *Cosbaea* is also distinct in having its outermost perianth parts considerably smaller than the largest parts. Smith (1947) hypothesised that the most primitive section is *Cosbaea*, and that the other two sections have been derived by processes of shortening of the filaments and enlargement of the connectives. Y.-W. Law (1996) raised the sections of *Kadsura* to the subgeneric level.

Two of the Malesian species belong to section *Kadsura*, viz. *K. heteroclita* (Roxb.) Craib and *K. philippinensis* Elmer; the remaining seven Malesian species all belong to section *Sarcocarpon*.

References: Law, Y.-W. (= Y. Liu), Fl. Reipubl. Pop. Sin. 30/1 (1966) 231–273. — Smith, A.C., Sargentia 7 (1947) 1–224.

KEY TO THE SPECIES

- 1a. Leaf margins entire or denticulate. Stamens with connectives that are broader than thick, so that thecae of adjacent stamens are contiguous 2
- b. Leaf margins entire. Stamens with connectives that are as broad as thick, so that thecae of adjacent stamens are not contiguous 3
- 2a. Perianth segments 10–17. Stamens 39–62(–72). Carpels 28–47 **4. *K. heteroclita***
- b. Perianth segments 10–12. Stamens 24–42. Carpels 17–36 **7. *K. philippinensis***
- 3a. Stamens 15–32. Carpels 18–68; pseudostyles narrow, subulate 4
- b. Stamens 21–57. Carpels 40–200(–300); pseudostyles broad with subpeltate pseudostigmas 5

- 4a. Leaves small, (5.5–)6.5–13(–14.5) by (2.5–)3–5.5(–6) cm, with (3–)4–6(–9) pairs of secondary veins. Flower peduncle comparatively long, (2–)4–11(–15) mm **5. *K. lanceolata***
- b. Leaves comparatively large, (10.5–)12–17.5(–21.5) by 6.5–11(–15) cm, with (5–)7–8(–9) pairs of secondary veins. Flower peduncle short, 0–2(–5) mm **2. *K. borneensis***
- 5a. Leaves broadly ovate, with long acuminate apex; lamina length:width ratio (1.7–)1.8–2.6(–2.7). Outer perianth segments generally large, 4.0–8.9 by 2.3–7.3 mm, innermost slightly reduced to 0.4–0.7 of length of largest **1. *K. acsmithii***
- b. Leaves elliptic to ovate, with acute to (short-)acuminate apex; lamina length:width ratio (1.1–)1.4–2.1(–3.0). Outer perianth segments generally smaller, 1.5–3.8 by 2.0–4.7 mm, innermost highly reduced to 0.1–0.4 of length of largest 6
- 6a. Flower peduncles comparatively thick, (1.1–)1.7–2.2(–2.8) mm. Outer perianth segments broad, length:width ratio 0.6–0.8 7
- b. Flower peduncles comparatively thin, 0.5–1.3(–2.1). Outer perianth segments narrow, length:width ratio 0.7–1.2 8
- 7a. Carpels numerous, 100–200(–300) **6. *K. marmorata***
- b. Carpels few, 35–40 **3. *K. celebica***
- 8a. Leaf intercostal venation indistinct adaxially, prominent abaxially. Berries small, (3.6–)6.8–10.9(–11.8) by (3.3–)6.1–10.1(–12.0) mm, subglobose with length:width ratio of 0.9–1.3, borne on stipes (1.8–)2.9–10.8(–15.2) mm long **9. *K. verrucosa***
- b. Leaf intercostal venation prominent both adaxially and abaxially. Berries comparatively large, 9.5–22(–30) by 6.5–14(–17.5) mm, elongate with length:width ratio of 1.2–1.8(–2.1), sessile **8. *K. scandens***

1. *Kadsura acsmithii* R.M.K. Saunders

Kadsura acsmithii R.M.K. Saunders, *Blumea* 42 (1997) 109. — Type: *Chai S 33578* (L holo; K, KEP, MO, SAN).

Woody vines. *Leaves* papyraceous to coriaceous, (5–)8–20(–29) µm thick; lamina elliptic to ovate, (11–)13.5–18.5 by 5.5–10.5 cm, length:width ratio (1.7–)1.8–2.6(–2.7); primary vein variably slightly to highly impressed above, (very) prominent below; secondary veins (3–)4–6 pairs, (slightly) arcuate; base acute to obtuse (occasionally cuneate); apex acute to long acuminate; margin entire; petiole 20–35(–41) mm long, (0.1–)1.3–2.5(–2.9) mm diameter. *Flowers* either borne solitary in axils of leaves or in axils of fugaceous bracts, occasionally cauliflorous; peduncle 5–35(–43) mm long, 0.7–1.9(–2.2) mm diameter. *Perianth segments* (9–)12–17, outer segments pale (yellowish-) green, tinged red, innermost pink to deep red; outermost perianth segment generally ovate, rarely obovate, 4.0–8.9 by 2.3–7.3 mm, length:width ratio 1.2–2.3, reduced to 0.4–0.6 of length of largest; innermost perianth segment ovate, elliptic or obovate, 4.1–8.5 by 2.4–5.0(–6.0) mm, length:width ratio (1.1–)1.3–1.8, reduced to 0.4–0.7 of length of largest; largest perianth segment generally ovate, rarely elliptic or obovate,

10.1–14.6 by 7.9–11.3 mm, length: width ratio 1.2–1.6. *Male flowers* with 22–53 stamens, pink to red, anthers \pm sessile, closely appressed in subglobose to ellipsoid head, 4.5–5.6 mm diameter, connectives broad, with dorso-lateral thecae so that thecae of adjacent stamens not contiguous. *Female flowers* with 35–110 carpels, gynoecium c. 5.7 mm diameter; ovaries 1.1–1.3 by 0.8–0.9 mm, length: width ratio 1.3–1.6; pseudostyle \pm broad with subpeltate pseudostigma. *Fruit* peduncle \pm elongated, 30–50 mm long; berries 35–110, ripening reddish-purple, 7–8 by 6–7.5 mm, length: width ratio 1.1–1.2, berries sessile, pericarp \pm uniform in thickness or slightly thicker distally. *Seeds* 1 to 2 per berry, discoid or reniform, 5.8–6.5 by 6.8–7 mm, length: width ratio 0.8–1.0.

Distribution — *Malesia*: Borneo (Sarawak and Kalimantan).

Habitat — Tropical to submontane forests, from sea level to 1160 m altitude.

2. *Kadsura borneensis* A.C. Sm.

Kadsura borneensis A.C. Sm., Sargentia 7 (1947) 205. — Type: *Clemens 34425* (UC holo; A, K, L), Sabah, Mt Kinabalu.

Woody vines. *Leaves* highly coriaceous, 17–22 μ m thick; lamina elliptic to ovate, (10.5–)12–17.5(–21.5) by 6.5–11(–15) cm, length: width ratio (1.1–)1.5–1.9(–2.2); primary vein (highly) impressed above, very prominent below; secondary veins (5–)7–8 (–9) pairs, arcuate; base obtuse to truncate; apex acute to acuminate; margin entire; petiole (14.5–)16.5–32 mm long, 1.6–3.6 mm diameter. *Flowers* either borne solitary in axils of leaves or in axils of fugaceous bracts, on young growth; peduncle very short, 0–1.9 (–4.4) mm long. *Perianth segments* 12–20, yellow; outermost perianth segment ovate, 0.6–5.2 by 0.8–5.2 mm, length: width ratio 0.8–1.0, highly reduced to 0.1–0.4 of length of largest; innermost perianth segment elliptic, 2.1–10.0 by 1.6–6.0 mm, length: width ratio 1.2–1.7, reduced to 0.4–0.8 of length of largest; largest perianth segment generally elliptic, 5.8–12.3 by 4.0–11.7 mm, length: width ratio 1.0–1.6. *Male flowers* with 18–28 stamens, pink, anthers \pm sessile, closely appressed in subglobose to ellipsoid head, 2.0–4.7 mm diameter, connectives broad, with dorso-lateral thecae so that thecae of adjacent stamens not contiguous. *Female flowers* with c. 35 carpels, pink; ovaries c. 2.2 by 1.8 mm, length: width ratio c. 1.2; the pseudostyle subulate, without pseudostigma. *Fruit* with c. 35 berries, ripening reddish-purple, (10.5–)14–22(–24) by (9–)9.5–11.5 (–12.5) mm, length: width ratio (1.0–)1.3–2.3, berries sessile, pericarp greatly thickened distally, with basal locule and seeds. *Seeds* 1 per berry, reniform, c. 7.4 by 8.0 mm, length: width ratio c. 0.9.

Distribution — *Malesia*: Borneo (Sabah, in vicinity of Mt Kinabalu).

Habitat — Tropical to montane forests, to 2000 m altitude.

Note — The pollen morphology of *Kadsura borneensis* is described in detail by Pragowski, World Pollen Spore Fl. 5 (1976) 1–32.

3. *Kadsura celebica* A.C. Sm.

Kadsura celebica A.C. Sm., Sargentia 7 (1947) 202–203. — Type: *Sarasin 584* (K holo), Celebes, Minahasa.

Woody vines. *Leaves* subcoriaceous; lamina ovate, c. 13 by 9 cm, length: width ratio c. 1.5; primary vein \pm plane above, prominent below; secondary veins 5 or 6 pairs, arcuate; base obtuse to truncate; apex acute to short acuminate; margin entire; petiole c. 15 mm long, c. 2 mm diameter. *Flowers* borne solitary in axils of leaves (occasionally with secondary flower borne in axil of prophyll), possibly also in axils of fugaceous bracts; peduncle c. 15 mm long, 1.7–1.8 mm diameter. *Perianth segments* c. 12; outermost perianth segment c. 2.5 by 3.7 mm, length: width ratio c. 0.7, highly reduced to 0.2 of length of largest; innermost perianth segment c. 9.5 by 8 mm, length: width ratio c. 1.2, slightly reduced to c. 0.8 of length of largest; largest perianth segment c. 12.5 by 8 mm, length: width ratio c. 1.5–1.6. *Male flowers* with c. 35 stamens, anthers \pm sessile, closely appressed in subglobose to ellipsoid head, c. 6.0 mm diameter, connectives broad, with dorso-lateral thecae so that thecae of adjacent stamens not contiguous. *Female flowers* with c. 40 carpels, gynoecium c. 9 mm diameter; pseudostyle irregularly broad with subpeltate pseudostigma. *Fruit* and *seed* not seen.

Distribution — Only known from type collection which bears no notes on habitat etc.

4. *Kadsura heteroclita* (Roxb.) Craib

Kadsura heteroclita (Roxb.) Craib, Fl. Siam. Enum. 1 (1931) 28; A.C. Sm., Sargentia 7 (1947) 187; Keng in Fl. Thailand 2 (1972) 113. — *Uvaria heteroclita* Roxb., Hort. Beng. (1814) 43, nom. nud.; Fl. Ind., ed. 2, 2 (1832) 455; Griff., Notul. Pl. As. 4 (1854) 711. — Type: *M. R. Smith s.n.*, 1812 (BM holo), India, Silhet.

Kadsura roxburghiana Arn., Jard. Mag. Zool. Bot. 2 (1838) 546; King, J. As. Soc. Beng. 58, ii (1889) 376; Ann. Bot. Gard. Calcutta 3 (1891) 222. — Type: *F. de Silva s.n.* (Wallich, Cat. no. 4987) (K lecto; A, NY).

Kadsura scandens var. *cuspidata* Blume ex Koord., Exk. Fl. Java 2 (1912) 242, pro syn.

Kadsura parvifolia A. Agostini, Atti Reale Accad. Fisiocrit. Siena, X, 1 (1926) 193. — Type: *Beccari* 367 (FI-B holo; K, L), Sumatra, Mt Singalan.

Woody vines. *Leaves* \pm papyraceous, (3–)4–11(–14) μ m thick; lamina elliptic, rarely ovate-elliptic, (6.5–)7–13(–14.5) by (2–)3–6.5(–7.5) cm, length: width ratio (1.7–)1.8–2.8(–3.2); primary vein (slightly) impressed above, (slightly) prominent below; secondary veins (4–)5–8(–10) pairs, straight to slightly arcuate; base cuneate, rarely obtuse, often short-attenuate; apex acute to acuminate; margin entire, rarely denticulate, 0(–8) teeth; petiole (8–)10–19(–23) mm long, (0.5–)0.7–1.7(–1.9) mm diameter. *Flowers* borne solitary in axils of leaves, occasionally with secondary flower borne in axil of prophyll, always on young growth; peduncle length highly variable, 1–6.5(–42.5) mm long, (0.6–)0.7–1.2(–2.4) mm diameter. *Perianth segments* 10–17, white, cream or yellow; outermost perianth segment ovate, 1.1–2.6(–3.2) by 1.7–2.5(–3.5) mm, length: width ratio 0.6–1.0(–1.2), highly reduced to 0.2–0.4 of length of largest; innermost perianth segment elliptic to ovate, (1.8–)3.2–5.7(–7.5) by 1.1–4.1 mm, length: width ratio (1.3–)1.6–2.5(–2.8), slightly reduced to (0.3–)0.6–0.9 of length of largest; largest perianth segment ovate (rarely elliptic or orbiculate), 5.4–7.5(–10.9) by (3.6–)4.5–6.5(–9.4) mm, length: width ratio (1.0–)1.1–1.4(–1.6). *Male flowers* with 39–62(–72) stamens, red, absent from apex of torus, anthers \pm sessile, closely appressed in subglobose to ellipsoid head, 2.0–4.5 mm diameter, connectives broad, with lateral thecae so

that the thecae of adjacent stamens contiguous; pollen hexacolpate. *Female flowers* with 28–47 free carpels, green, gynoecium 3.2–4.1 mm diameter; ovaries (1.3–)1.5–1.9 (–2.2) by 1.0–1.2(–1.9) mm, length: width ratio 1.0–1.7; pseudostyle broad with subpeltate pseudostigma. *Fruit* peduncle slightly elongated, 14–46 mm long; berries 28–41, ripening red, 19.4–24.2 by 7.9–11.2 mm, length: width ratio 2.1–3.0, berries sessile. *Seeds* 1 or 2 per berry, pyriform, discoid or reniform, 4.6–5.6 by 4.3–5.5 mm, length: width ratio 0.9–1.2.

Distribution — Southern China to north-east India, and in peninsular India, Sri Lanka and Andaman Islands. See A.C. Smith, *Sargentia* 7 (1947) 189. In *Malesia*: Sumatra, Malay Peninsula, Borneo.

Habitat — Submontane to montane forests, 800–2000 m altitude.

Note — Detailed descriptions of microsporogenesis [M.R. Vijayaraghavan & U. Dhar, *J. Arnold Arbor.* 56 (1975) 176–182], pollen structure [Vijayaraghavan & Dhar, l.c.; Pragłowski, *World Pollen Spore Fl.* 5 (1976) 1–32] and carpel structure [Vijayaraghavan & Dhar, *Bot. Jahrb. Syst.* 98 (1977) 273–277] have been published.

5. *Kadsura lanceolata* King

Kadsura lanceolata King, *J. As. Soc. Beng.* 58, ii (1889) 376; Ridl., *Fl. Malay Penins.* 1 (1922) 21; A. C. Sm., *Sargentia* 7 (1947) 203–204. — Type: *King's coll. (Kunstler)* 3463 (K lecto).

Kadsura scandens auct. non Blume: Ridl., *Sarawak Mus. J.* 1, 3 (1913) 72; A. Agostini, *Atti Reale Accad. Fisiocrit. Siena*, X, 1 (1926) 194.

Kadsura ultima A.C. Sm., *Sargentia* 7 (1947) 207. — Type: *Robinson 2005* (US holo; K, L), Ambon.

Woody vines. *Leaves* coriaceous, (5–)7–22(–27) μ m thick; lamina (ovate-)elliptic, rarely ovate, (5.5–)6.5–13(–14.5) by (2.5–)3–5.5(–6) cm, length: width ratio (1.3–)1.6–2.7(–2.9); primary vein (slightly) impressed above, prominent below; secondary veins (3–)4–6(–9) pairs, slightly arcuate; base obtuse, rarely truncate (cuneate in younger leaves); apex acuminate, rarely acute; margin entire; petiole (5–)7–18(–22) mm long, 0.9–2.2(–2.6) mm diam. *Flowers* borne solitary in axils of leaves, occasionally with secondary flower borne in axil of prophyll, always on young growth; peduncle (2–)4–11(–15) mm long, (0.3–)0.7–1.3(–1.6) mm diameter. *Perianth segments* 7–12 (–14), outer segments pink to dark red, inner segments cream to bright yellow; outermost perianth segment ovate, 1.0–2.5(–8.0) by 1.2–2.5(–7.3) mm, length: width ratio 0.6–1.0 (–1.3), highly reduced to 0.1–0.4(–0.9) of length of largest; innermost perianth segment elliptic to obovate, (1.6–)4.0–7.8(–11.0) by (0.8–)2.3–4.3(–8.1) mm, length: width ratio 1.2–1.7(–2.7), slightly reduced to (0.3–)0.7–1.0 of the length of the largest; largest perianth segment shape variable, generally elliptic to ovate, 5.0–7.8 (–13.5) by 3.5–6.3(–14.7) mm, length: width ratio 0.9–1.5(–2.2). *Male flowers* with 15–32 stamens, anthers \pm sessile, closely appressed in subglobose to ellipsoid head, 2.3–6.2 mm diameter, connectives broad, with dorso-lateral thecae so that thecae of adjacent stamens not contiguous. *Female flowers* with 18–68 carpels, gynoecium 2.5–5.0 mm diameter; ovaries 0.9–1.5(–1.6) by 0.6–1.0(–1.2) mm, length: width ratio (0.8–)0.9–1.4(–2.5); pseudostyle subulate, without pseudostigma. *Fruit* peduncle not markedly elongated, 4–14 mm long; berries 18–32 (possibly more), ripening red or yellow, 5.1–

6.6 by 3.8–6.0 mm, length: width ratio 1.0–1.7, berries sessile, pericarp \pm uniform in thickness or slightly thicker distally. *Seeds* 1–3 per berry, discoid to pyriform, (3.7–)4.1–4.5(–5.2) by (3.0–)3.4–5.0 mm, length: width ratio 0.8–1.3.

Distribution — *Malesia*: Sumatra, Malay Peninsula, Borneo, Celebes, and Moluccas (Halmahera and Ambon).

Habitat — Tropical to submontane forests (to 1400 m altitude), occasionally montane and subalpine forests (to 2900 m altitude).

Note — Accounts of the structure of the leaf cuticle and pollen of *Kadsura lanceolata* have been published by H. S. Rao [Proc. Ind. Acad. Sci., B 9 (1939) 99–116 + 21 pl.] and Praglowski [World Pollen Spore Fl. 5 (1976) 1–32], respectively.

6. *Kadsura marmorata* (Hend. & A. Hend.) A. C. Sm.

Kadsura marmorata (Hend. & A. Hend.) A. C. Sm., Sargentia 7 (1947) 196. — *Sphaerostema marmoratum* Hend. & A. Hend., Ill. Bouquet 2 (1859–61) pl. 40. — Lectotype: the plate mentioned.

Kadsura scandens auct. non Blume: Merr., Philipp. J. Sc., Bot. 2 (1907) 422.

Kadsura apoensis Elmer, Leaflet. Philipp. Bot. 8 (1915) 2748; Merr., Univ. Calif. Publ. Bot. 15 (1929) 60. — Type: *Elmer 11718* (GH lecto; A, E, F, K, L, MO, NY), Mt Apo, Mindanao.

Kadsura sulphurea Elmer, Leaflet. Philipp. Bot. 8 (1915) 2750. — Type: *Elmer 13505* (GH lecto; A, E, F, K, L, MO, NY, UC), Mt Urdaneta, Mindanao.

Kadsura clemensiae A. C. Sm., Sargentia 7 (1947) 206. — Type: *Clemens 22115* (A holo; K iso), Sarawak.

Woody vines. *Leaves* \pm coriaceous, (5–)8–15(–20) μ m thick; lamina elliptic to ovate, (10–)13–18(–21) by (5–)6–11(–18) cm, length: width ratio (1.1–)1.4–2.1(–3.0); primary vein slightly to highly impressed above, (very) prominent below; secondary veins (3–)5–6(–8), generally arcuate; base obtuse to truncate; apex acute to acuminate; margin entire; petiole (15–)19–33(–79) mm long, (1.4–)1.9–3.0(–4.7) mm diameter. *Flowers* either borne solitary in axils of leaves or in axils of fugaceous bracts, occasionally cauliflorous, often growing as glomerules on trunk; peduncle (2.5–)5–43 mm long, (1.1–)1.7–2.2(–2.8) mm diameter. *Perianth segments* 12–21, yellowish, outermost segments sometimes greenish; outermost perianth segment ovate, 1.8–8.9 by 2.8–7.3 mm, length: width ratio 0.6–0.8, highly reduced to 0.2–0.3 of length of largest; innermost perianth segment generally elliptic, (1.8–)6.5–10.5 by (0.8–)4.6–7.3 mm, length: width ratio 1.3–1.4(–2.3), reduced to (0.3–)0.5–0.8 of length of largest; largest perianth segment elliptic to ovate, (6.3–)9–13 by 6.1–9.7 mm, length: width ratio (1.0–)1.3–1.5. *Male flowers* with 38–53 stamens, anthers \pm sessile, closely appressed in subglobose to ellipsoid head, 7–8 mm diameter, connectives broad, with dorso-lateral thecae so that thecae of adjacent stamens not contiguous. *Female flowers* with 100–200 (to 300, fide Smith 1947: 197) carpels, gynoecium 5.7–7.5 mm diameter; ovaries 1.1–2.0 by 0.8–1.2 mm, length: width ratio 1.3–2.1; pseudostyle broad with subpeltate pseudostigma. *Fruit* with 100–200 berries (possibly more), ripening cream to dull yellow or red, (16–)19–39 by 6–14 mm, length: width ratio (1.4–)2.4–4.2(–5.6), berries sessile, pericarp greatly thickened distally, with basal locule and seeds. *Seeds* 1 or 2 per berry, discoid to pyriform, 5.0–8.6 by 4.6–5.2(–6.6) mm, length: width ratio 1.0–1.4(–1.8).

Distribution — *Malesia*: Borneo (Sabah, Sarawak), Philippines (Mindanao, Palawan).

Habitat — Tropical to submontane forests, to 1500 m altitude.

Notes — Stomatal characteristics of *Kadsura marmorata* are illustrated by Metcalfe [Anat. Dicot., ed. 2, 3 (1987) 83–89], and pollen structure by Praglowski [World Pollen Spore Fl. 5 (1976) 1–32].

7. *Kadsura philippinensis* Elmer

Kadsura philippinensis Elmer, Leafl. Philipp. Bot. 1 (1908) 277; A.C. Sm., Sargentia 7 (1947) 192. — Type: Elmer 8700 (A lecto; E), Luzon.

Kadsura paucidenticulata Merr., Philipp. J. Sc., Bot. 5 (1910) 176; A.C. Sm., Sargentia 7 (1947) 193. — Type: McGregor 8498 (K lecto; L, NY), Luzon.

Kadsura macgregorii Merr., Philipp. J. Sc., Bot. 5 (1910) 177. — Type: McGregor 8340 (destroyed), Luzon.

Kadsura sorsogonensis Elmer ex Merr., Enum. Philipp. Flow. Pl. 2 (1923) 153, pro syn.

Woody vines. *Leaves* ± papyraceous, (4–)5–7(–10) µm thick; lamina elliptic, rarely ovate-elliptic or ovate, (6.5–)7–10(–11.5) by 3–5(–6) cm, length: width ratio (1.7–)1.9–2.5(–2.7); primary vein plane to slightly impressed above, prominent below; secondary veins 5–6(–7) pairs, often indistinct due to presence of intersecondary veins, slightly arcuate; base cuneate to obtuse; apex acute to acuminate; margin entire to denticulate, 0–4 (–6) teeth; petiole (6.5–)7.5–15(–17) mm long, 0.8–1.4(–1.7) mm diameter. *Flowers* borne solitary in axils of leaves, always on young growth; peduncle (10–)15–32 mm long, 0.4–0.8(–0.9) mm diameter. *Perianth segments* 10–12, white or dull yellow; outermost perianth segment ovate, 1.2–1.8(–3.4) by 1.3–2.2(–4.1) mm, the length: width ratio (0.5–)0.8–1.1, highly reduced to 0.2–0.4 of length of largest; innermost perianth segment elliptic to ovate, (3.6–)4.3–5.5 by 2.5–2.9 mm, length: width ratio (1.3–)1.5–1.9(–2.2), slightly reduced to (0.4–)0.6–0.9 of length of largest; largest perianth segment orbicular to ovate, 4.2–10.6 by 4.7–8.4 mm, length: width ratio 0.9–1.1(–1.3). *Male flowers* with 24–42 stamens, absent from apex of torus, anthers ± sessile, closely appressed in subglobose to ellipsoid head, c. 2.6 mm diameter, connectives broad, with lateral thecae so that thecae of adjacent stamens contiguous; pollen hexacolpate. *Female flowers* with 17–36 free carpels, gynoecium c. 3.1 mm diameter; ovaries 1.0–3.0 by 0.7–2.8 mm, length: width ratio 1.0–1.3(–1.7); pseudostyle broad with subpeltate pseudostigma. *Fruit* peduncle slightly elongated, 28–38 mm long; berries 20–45, ripening white to brown, (2.6–)5.0–5.9 by (2.6–)3.1–3.6(–5.0) mm, length: width ratio 1.0–1.7, sessile or on short stipe, to c. 1.2 mm. *Seeds* 1 or 2 per berry, reniform, 2.6–4.2 by 3.4–4.7 mm, length: width ratio c. 0.8–0.9.

Distribution — *Malesia*: Philippines (Luzon and Mindanao).

Habitat — Submontane to montane forests, 850–2100 m altitude.

Note — Pollen structure is described by Wodehouse [Pollen Grains (1959) 340] and Praglowski [World Pollen Spore Fl. 5 (1976) 1–32].

8. *Kadsura scandens* (Blume) Blume

Kadsura scandens (Blume) Blume, Fl. Javae (1830) 9; King, J. As. Soc. Beng. 58, ii (1889) 375; Ann. Bot. Gard. Calc. 3, 2 (1891) 221, pl. 71; Ridl., J. Str. Br. Roy. As. Soc. 33 (1900) 38; Backer,

- Schoolfl. Java (1911) 16; Koord., Exk. Fl. Java 2 (1912) 242; Ridl., Fl. Malay Penins. 1 (1922) 20; A. C. Sm., Sargentia 7 (1947) 199; Backer & Bakh. f., Fl. Java 1 (1964) 99; Keng in Fl. Thailand 2 (1972) 114; Conc. Fl. Sing. (1990) 9; R. M. K. Saunders, Gard. Bull. Sing. (in press). — *Sarcocarpon scandens* Blume, Bijdr. (1825) 21. — *Kadsura scandens* var. *normalis* Kuntze, Rev. Gen. Pl. 1 (1891) 6. — Type: *Blume s.n.* (L lecto; K, NY), Java, Mt Gedeh/Pangrango.
- Kadsura cauliflora* Blume, Fl. Javae (1830) 11; Backer, Schoolfl. Java (1911) 17. — *Kadsura scandens* var. *cauliflora* (Blume) Kuntze, Rev. Gen. Pl. 1 (1891) 6. — Type: *Blume s.n.* (L lecto; K), Java, Mt Burangrang.
- Kadsura scandens* var. *intermedia* Kuntze, Rev. Gen. Pl. 1 (1891) 6. — Type: *Kuntze 5210* (NY lecto), Java, Sagaranten-Rambai.
- Schizandra ovalifolia* Parment., Bull. Sc. Fr. Belg. 27 (1896) 237, 312. — Type: *Beccari 667* (MEL holo; K, L), Sumatra, Padang.
- Kadsura wallichii* Korth. ex Koord., Exk. Fl. Java 2 (1912) 242, pro syn.

Woody vines. *Leaves* papyraceous to coriaceous, 5–16(–19) µm thick; lamina elliptic to ovate, (9–)10–15(–21) by (4.5–)5–9(–15) cm, length: width ratio (1.3–)1.4–2.1 (–2.4); primary vein variably plane to highly impressed above, (very) prominent below; secondary veins 4–6(–8) pairs, (slightly) arcuate; base obtuse to truncate (cuneate in younger leaves); apex acute to acuminate; margin entire; petiole (7.5–)11.5–30(–48) mm long, 1.2–2.3(–2.8) mm diameter. *Flowers* either borne solitary in axils of leaves (occasionally with secondary flower borne in axil of prophyll) or in axils of fugaceous bracts, occasionally cauliflorous; peduncle (4–)8–42(–70) mm long, 0.6–1.3 mm diameter. *Perianth segments* (7–)11–18, white, pale yellow or red, outer segments occasionally pale green, tinged red; outermost perianth segment generally ovate, 1.5–3.8 by 2.0–3.3 mm, length: width ratio 0.7–1.2, highly reduced to 0.1–0.4 of length of largest; innermost perianth segment (sub)elliptic, 4.3–7.3(–10.5) by 2.9–6.2 mm, length: width ratio (1.2–)1.5–2.1, reduced to 0.4–0.7(–0.9) of length of largest; largest perianth segment generally ovate, occasionally orbiculate or elliptic, (7.4–)9–16(–18.9) by (4.7–) 7.0–12.0(–14.3) mm, length: width ratio 1.0–1.6. *Male flowers* with 24–52 stamens, pink to dark red, anthers ± sessile, closely appressed in subglobose to ellipsoid head, 4.1–6.0 mm diameter, connectives broad, with dorso-lateral thecae so that thecae of adjacent stamens not contiguous. *Female flowers* with 50–82 (–110) carpels, gynoecium 4.9–6.5 mm diameter; ovaries 1.8–2.7 by 0.9–1.4 mm, length: width ratio (1.6–)1.9–2.6(–3.0); pseudostyle broad with subpeltate pseudostigma. *Fruit* peduncle not markedly elongated, 21–25 mm long; berries 40–93 (possibly more), ripening red, 9.5–22(–30) by 6.5–14(–17.5) mm, length: width ratio 1.2–1.8 (–2.1), berries sessile, pericarp greatly thickened distally, with basal locule and seeds. *Seeds* 1 or 2 per berry, pyriform, discoid or reniform, (4.5–)5.5–8.5(–10) by (4–)5–9 (–11) mm, length: width ratio 0.8–1.1(–1.5). — **Fig. 1.**

Distribution — *Malesia*: Sumatra, Malay Peninsula, Java and Bali.

Habitat — Tropical to montane forests, to 2400 m altitude.

Uses — *Kadsura scandens* is reported to have a variety of medicinal uses. Decoctions of the roots and/or stems are used as a lotion to combat rheumatism or as an expectorant; the sap is drunk as a remedy for urinary problems, abdominal pains and diarrhoea, or applied to alleviate skin diseases; and the bark is further used to combat fever. See Burkill, Dict. Econ. Prod. Malay Penins. 2 (1966) 1296; K. Heyne, Nutt. Pl. Indon.,



Fig. 1. *Kadsura scandens* (Blume) Blume. a. Flowering branch; b. gynoecium; c. isolated carpel (lateral view); d. androecium; e. isolated stamen (lateral view); f. aggregate fruit of separate berries; g. seed (a: Ridley 6354; b, c: Nur 26103; d, e: Korthals s. n.; f: redrawn from Van Steenis, Mountain Fl. Java (1972) f. 29.3; g: Wirawan 134). Drawing by H.L. Wilks.

ed. 3 (1950) 626; L.M. Perry, *Medic. Pl. S. & SE. Asia* (1980) 381–382. The fruit is also reported to be edible, although rather astringent (Burkill 1966; Heyne 1950).

Note — Cuticular features are discussed by H.S. Rao [*Proc. Ind. Acad. Sc.*, B 9 (1939) 99–116 + 21 pl.], and pollen structure by Wodehouse [*Pollen Grains* (1959) 340] and Praglowski [*World Pollen Spore Fl.* 5 (1976) 1–32].

9. *Kadsura verrucosa* (Gagnep.) A.C. Sm.

Kadsura verrucosa (Gagnep.) A.C. Sm., *Sargentia* 7 (1947) 195. — *Schisandra verrucosa* Gagnep. in *Fl. Indochine*, Suppl. 1 (1938) 56, nom. inval., '*Schizandra*'; *Not. Syst. Mus. Nat. Paris* 8 (1939) 66, '*Schizandra*'. — Type: *Poilane 25429* (P lecto; A, K).

Kadsura cauliflora auct. non Blume: King, *J. As. Soc. Beng.* 58, ii (1889) 375; *Ann. Roy. Bot. Gard. Calc.* 3 (1891) 222; *Ridl., Fl. Malay Penins.* 1 (1922) 20; A. Agostini, *Atti Reale Accad. Fisiocrit. Siena*, X, 1 (1926) 194, pro parte.

Woody vines. *Leaves* coriaceous, (5–)8–12(–20) μ m thick; lamina elliptic to ovate, (8.5–)10–15(–21) by (4–)4.5–12.5(–14) cm, length: width ratio (1.1–)1.4–2.1(–2.8); primary vein plane to slightly impressed above, (very) prominent below; secondary veins (4–)5–7(–8) pairs, arcuate; base obtuse to truncate; apex acute to acuminate; margin entire, rarely subdentate; petiole (14–)15.5–30(–60) mm long, (1.1–)1.3–3.0(–3.7) mm diameter. *Flowers* either borne solitary in axils of leaves or in axils of fugaceous bracts, occasionally cauliflorous, growing as glomerules on trunk; peduncle 11–27(–35) mm long, 0.5–1.3(–2.1) mm diameter. *Perianth segments* 12–15, yellow, cream or pink; outermost perianth segment ovate, 2.0–3.5 by 1.8–4.7 mm, length: width ratio 0.7–1.2, highly reduced to 0.1–0.2 of length of largest; innermost perianth segment shape variable, generally elliptic, 5.8–8.0(–15.9) by 3.4–6.2(–10.3) mm, the length: width ratio 1.3–1.7, reduced to 0.4–0.7 of length of largest; largest perianth segment generally ovate, 11.3–15.0(–21.5) by 9.6–14.0(–19.7) mm, length: width ratio 1.1–1.3. *Male flowers* with 40–57 stamens, anthers \pm sessile, closely appressed in subglobose to ellipsoid head, 4.0–5.8 mm diameter, connectives broad, with dorso-lateral thecae so that thecae of adjacent stamens not contiguous. *Female flowers* with 47–55 carpels, gynoecium c. 5 mm diameter; ovaries 1.7–3.8 by 0.5–1.7 mm, length: width ratio 2.1–3.8; pseudostyle broad with subpeltate pseudostigma. *Fruit* peduncle \pm elongated, 20–50 mm long; berries 30–50, ripening red or yellow, (3.6–)6.8–10.9(–11.8) by (3.3–)6.1–10.1(–12.0) mm, length: width ratio 0.9–1.3, berries borne on stipes, (1.8–)2.9–10.8(–15.2) mm long, articulate at apex of stipe, pericarp \pm uniform in thickness, not distally thickened. *Seeds* (1 or) 2 per berry, discoid to reniform, 5–6.3(–6.6) by (3.8–)5.0–6.6 (–7.8) mm, length: width ratio 0.8–1.1.

Distribution — Indochina; *Malesia*: Sumatra, Malay Peninsula, and Java.

Habitat — Tropical to submontane forests, up to 1300 m altitude, rarely montane to 2000 m altitude.

INSUFFICIENTLY KNOWN

Kadsura billitonensis A. Agostini, *Atti Reale Accad. Fisiocrit. Siena*, X, 1 (1926) 193.

— Type: *Riedel s.n.* (FI-B holo), Belitung (Billiton). Not identifiable.

SCHISANDRA

Schisandra Michx., Fl. Bor.-Amer. 2 (1803) 218, t. 47, nom. conserv.; DC., Syst. 1 (1818) 544; A.C. Sm., Sargentia 7 (1947) 86; Backer & Bakh. f., Fl. Java 1 (1964) 99. — Type species: *Schisandra coccinea* Michx. [syn. *S. glabra* (Brickell) Rehder].

Sphaerostema Blume, Bijdr. (1825) 22. — Type species: *Sphaerostema axillare* Blume [= *Schisandra propinqua* (Wall.) Baill. subsp. *axillaris* (Blume) R.M.K. Saunders].

Woody vines; monoecious. *Leaves* alternate on long shoots or clustered on short shoots, exstipulate; lamina papyraceous to coriaceous, elliptic to ovate, apex acute to acuminate, base generally acute to decurrent, margins denticulate to entire, pinnate venation; petioles with groove on adaxial surface. *Flowers* generally solitary and axillary, occasionally in clusters of up to 8, sometimes ramiflorous. *Perianth segments* 5–20, imbricate at anthesis, outermost and innermost segments \pm reduced, elliptic to suborbicular or obovate, white, (orange-)yellow, pink, or (purple-)red. *Androecium* of few to numerous (4–60) stamens; stamens sometimes \pm free but fused at base of filaments, sometimes fused to form subglobose carnosose mass with thecae embedded in cavities, sometimes fused to form flattened pentagonal mass ('staminal shield'); pollen grains tri- or hexacolpate, distally syncolpate. *Gynoecium* of numerous (12–120) carpels; receptacle cylindrical or conical, distinctly longer than wide; stigmatic crest forming subulate 'pseudostyle', lacking 'pseudostigma'; ovary with 2 (or 3) ventrally attached ovules. *Fruit* an aggregate of berries attached to elongated receptacle; berries ellipsoid to ob-ovoid, ripening red; pedicel not enlarged in fruit. *Seeds* (1–)2(–3), smooth to rugulose, hilum lateral. — **Fig. 2.**

Distribution — There are c. 25 species in the genus, with an extensive distribution from southern Sakhalin in the north-east to the Himalayas in the west; the centre of diversity lies in Assam and southern China. The genus shows two major disjunctions: two species, *S. propinqua* (Wall.) Baill. and *S. elongata* (Blume) Baill., occur in Java and Bali; and *S. glabra* (Brickell) Rehder is endemic to the south-east United States [A.C. Smith, Sargentia 7 (1947) 1–224]. In *Malesia*: Java and Bali (2 species).

Habitat & Ecology — As for the family.

Vegetative anatomy — In addition to the references given in the discussion of the morphology and anatomy of the family, the following aspects of the vegetative anatomy of *Schisandra* have received particular attention: stomatal structure and development (Rao 1939; Jalan 1962); nodal anatomy (Jalan 1968a); crystalliferous sclereids (Jalan 1968b); ethereal oil cells (Jalan 1965); and mucilage cells (Jalan 1975).

References: Jalan, S., Phytomorphology 12 (1962) 239–242; Curr. Sci. 18 (1965) 527–528; Bot. Jahrb. 88 (1968a) 311–316; Beitr. Biol. Pflanzen 44 (1968b) 277–288; J. Ind. Bot. Soc. 54 (1975) 62–65. — Rao, H.S., Proc. Ind. Acad. Sci., B 9 (1939) 99–116.

Floral morphology — The female flowers of *Schisandra* are characterised by carpels with subulate stigmatic crests, and cylindrical or conical receptacles that are markedly longer than wide and become highly elongated in the fruit. The male flowers show great variation in androecial structure: the most primitive androecia consist of a large number

of essentially free stamens that are only fused at the base of the filaments. According to Smith (1947), three distinct evolutionary trends are evident in the genus: 1) reduction of the number of stamens, ultimately giving rise to an extreme of only 4–5 in *S. chinensis* (Turcz.) Baill.; 2) complete fusion of the filaments to form a carnosse mass with the anthers embedded in cavities; and 3) fusion of the filaments to form a 'staminal shield' of five stamens, with the thecae borne on the lower (morphologically dorsal) margins of the connectives. The androecial variation was used by Smith (1947) as the basis for his sectional classification of the genus (discussed below). Floral ontogeny is described and illustrated in detail by Tucker & Bourland (1994).

References: Smith, A.C., *Sargentia* 7 (1947) 1–224. — Tucker, S.C. & J.A. Bourland, *Pl. Syst. Evol.*, Suppl. 8 (1994) 137–158.

Cytology — Six species of *Schisandra* have been examined cytologically, although none of these species occur in Malesia. Most reports are of $n = 14$ (Whitaker 1933; Ehrendorfer et al. 1968; Stone 1968; Ratter & Milne 1976; Sandhu et al. 1989) and $2n = 28$ (Janaki-Ammal, unpubl., cited in Darlington & Wylie 1955; Stone 1965, 1968; Okada 1975; Singhal et al. 1980; Gill et al. 1982; Chen et al. 1993; Wu & Huang 1995), although Bostick (1965) reports $n = 13$ for *S. glabra* (syn. *S. coccinea*). Other studies have revealed a diploid cytotype of $n = 7$ for *S. grandiflora* (Wall.) Hook. f. & Thoms. (Malla et al. 1977; Sandhu et al. 1989). The base number for the genus is therefore regarded as $x = 7, 13$.

References: Bostick, P.E., *Sida Contrib. Bot.* 2 (1965) 165–168. — Chen, R.-Y., et al., *Chromosome Atlas of Chinese Principal Economic Plants* 1 (1993) 319–320. — Darlington, C.D. & A.P. Wylie, *Chromosome Atlas of Flowering Plants* (1955) 14. — Ehrendorfer, F., et al., *Taxon* 17 (1968) 337–353. — Gill, B.S., et al., in G.S. Paliwal, *The Vegetational Wealth of the Himalayas* (1982) 497–515. — Malla, S.B., et al., in Á. Löve, *Taxon* 26 (1977) 443–452. — Okada, H., *J. Sci. Hiroshima Univ. B (Bot.)* 15 (1975) 115–200. — Ratter, J.A. & C. Milne, *Notes Roy. Bot. Gard. Edinb.* 35 (1976) 143–145. — Sandhu, P.S., et al., *Curr. Sci.* 58 (1989) 925–926. — Singhal, V.K., et al., in Á. Löve, *Taxon* 29 (1980) 355–357. — Stone, D.E., *Madroño* 18 (1965) 122–126; *J. Elisha Mitchell Sci. Soc.* 84 (1968) 351–356. — Whitaker, T.W., *J. Arnold Arbor.* 14 (1933) 376–385. — Wu, Z. & C. Huang, *Guihaia* 15 (1995) 47–51.

Uses — *Schisandra* is not very important economically, although the North Asian species *S. chinensis* and *S. propinqua* are used for various medicinal purposes [L.M. Perry, *Medic. Pl. S. & SE Asia* (1980) 381–382].

Taxonomy — The most comprehensive taxonomic revision of *Schisandra* is by A.C. Smith (1947), who accepted 25 species. Smith recognised four different androecial types in the genus, which he used as the primary criterion for the delimitation of sections, as follows:

Sect. *Pleiostema* A.C. Sm., with few to numerous essentially free stamens, arranged in irregular whorls on an elongated column or torus;

Sect. *Maximowiczia* (Rupr.) Nakai, with the filaments fused into a short column, bearing few sessile anthers at its apex;

Sect. *Schisandra* ('*Euschisandra*'), with the androecium composed of a flattened pentagonal shield with five radiating anthers bearing thecae on the dorsal margin;

Sect. *Sphaerostema* (Blume) Nakai, with the androecium composed of a subglobose or ellipsoid carnose mass, derived by the fusion of filaments, with anthers borne in cavities on the surface.

Smith hypothesised that the most primitive section was *Pleiostema*, and that the other sections have been derived by processes of filament fusion and the reduction in stamen number. Although the delimitation of the sections was primarily based on androecial structure, there is also an imperfect correlation with seed coat structure.

Y.-W. Law (1996) proposed a revised supraspecific classification for the genus, involving both the raising of the sections to subgeneric level, and the recognition of two new subgenera, viz.: '*Sinoschisandra*' for those species (previously classified in sect. *Pleiostema*) which possess a sterile 'shield' over the apex of the torus; and '*Plenischisandra*' solely for *S. plena* A.C. Sm., which differs from the other species previously classified in sect. *Sphaerostema* in possessing sessile anthers.

The two Malesian species belong to different supraspecific taxa: *S. elongata* (Blume) Baill. belongs to sect. *Pleiostema* sensu Smith (= subg. *Pleiostema* sensu Law), whereas *S. propinqua* subsp. *axillaris* (Blume) R.M.K. Saunders belongs to sect. *Sphaerostema* sensu Smith (= subg. *Sphaerostema* sensu Law).

References: Law, Y.-W. (= Y. Liu) in Fl. Reipubl. Pop. Sin. 30, 1 (1996) 231–273. — Smith, A.C., Sargentia 7 (1947) 1–224.

KEY TO THE SPECIES

- 1a. Leaves comparatively narrow (length:width ratio 2.2–2.6–3.2), \pm coriaceous. Flowering pedicel short, 0–5–11 mm, fruiting pedicel 3–12 mm. Androecium a fused mass of 10–12–17 stamens, with anthers embedded in cavities **1. *S. propinqua* subsp. *axillaris***
- b. Leaves comparatively broad (length:width ratio 1.7–2.0–2.3), papyraceous or occasionally membranaceous. Flowering pedicel long, 28–38–63 mm, fruiting pedicel long, 40–60 mm. Androecium of 27–30 stamens, fused only at the base of the filaments **2. *S. elongata***

1. *Schisandra propinqua* (Wall.) Baill. subsp. *axillaris* (Blume) R.M.K. Saunders

Schisandra propinqua (Wall.) Baill. subsp. *axillaris* (Blume) R.M.K. Saunders, Edinb. J. Bot. (in press).

— *Sphaerostema axillare* Blume, Bijdr. Fl. Ned. Ind. (1825) 22, '*axillaris*'; Fl. Javae (1830) 14, t. 3.

— *Sphaerostemma axillare* Blume ex G. Don, Gen. Hist. Dichlam. Pl. 1 (1831) 101, '*axillaris*'. —

Schisandra axillaris (Blume) Hook. f. & Thomson in Hook. f., Fl. Brit. India 1 (1872) 45, '*Schizandra axillaris*'; Backer, Schoolfl. Java (1911) 16; A.C. Sm., Sargentia 7 (1947) 147; Backer & Bakh. f., Fl. Java 1 (1964) 99; Steenis, Mountain Fl. Java (1972) t. 29.4. — Type: *Blume s.n.* (BO lecto; K, L, NY), Java, Mt Tjareme.

Sphaerostema pyrifolium Blume, Fl. Javae (1830) 16, t. 4. — *Uvaria pyrifolia* Reinw. ex Blume, Fl. Javae (1830) 16, pro syn. — *Sphaerostemma pyrifolium* Blume ex Walp., Rep. Bot. Syst. 1 (1842) 92. — *Sphaerostemma pyrifolium* Blume ex Koord., Exk. Fl. Java 2 (1912) 243, pro syn., '*pirifolium*'. — Type: *Blume s.n.* (L lecto & iso), Java, Ciancur.

Sphaerostemma pyrifolium var. *denticulatum* Blume ex Koord., Exk. Fl. Java 2 (1912) 243, pro syn., 'pirifolium'.

Schizostigma axillare Hook. f. & Thomson ex Merr., Enum. Philipp. Flow. Pl. 2 (1923) 153, sphalm.

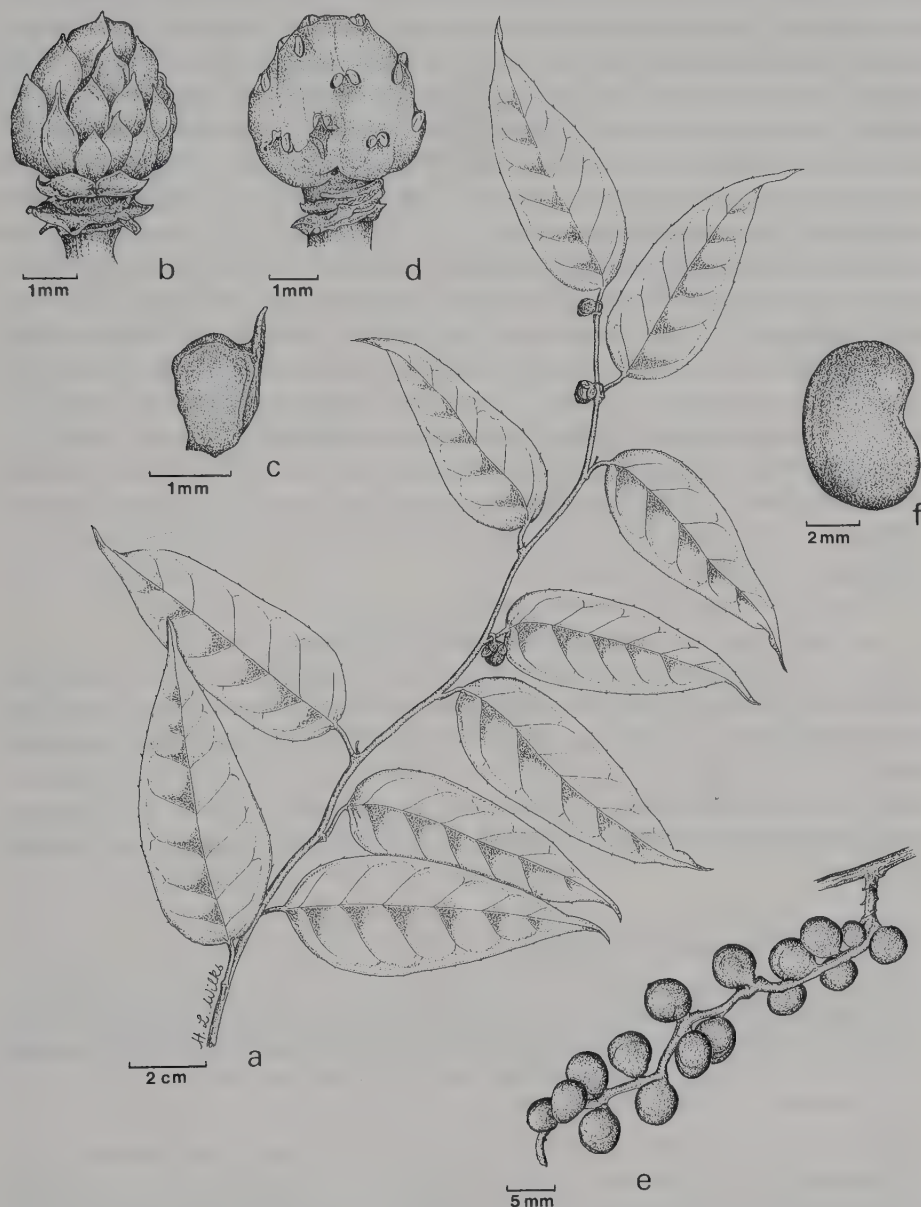


Fig. 2. *Schisandra propinqua* (Wall.) Baill. subsp. *axillaris* (Blume) R.M.K. Saunders. a. Flowering branch; b. gynoecium; c. isolated carpel (lateral view); d. androecium; e. aggregate fruit of separate berries; f. seed (a: Blume s.n.; b, c: Coert 944; d: Brinkman 874a; e, f: Backer 3656). Drawing by H.L. Wilks.

Woody vines, monoecious. *Leaves* coriaceous, 5–20 µm thick; lamina elliptic to ovate, 6–11.5 by 2–4.5(–5) cm, length: width ratio (2.0–)2.3–3.2(–3.5); primary vein plane to slightly impressed above, prominent to very prominent below; secondary veins (4–)5–6(–7) pairs, ± straight; base obtuse to truncate (acute in younger leaves), often short-decurrent; apex acute to acuminate; margin entire to denticulate, 0–8 teeth; petiole (8–)10–17(–21) mm long, (0.8–)1.0–1.5(–1.8) mm diameter. *Flowers* borne axillary to leaves on young growth, solitary; pedicel (2–)3–5(–12) mm long, 0.6–1.1 mm in diameter. *Perianth segments* 9–14, outer segments (green-)yellow, inner red; outermost perianth part ovate, 1.0–2.4 by 1.1–2.4 mm, length: width ratio 0.7–1.0(–1.5); innermost perianth part elliptic to ovate, (2.3–)3.5–4.0(–5.3) by 1.9–3.5 mm, length: width ratio 1.2–1.8; largest perianth part ovate, 4.3–7.8 by 4.1–6.0(–7.0) mm, length: width ratio 0.9–1.3; outermost perianth part highly reduced to 0.2–0.4 of length of largest; innermost perianth part reduced to 0.5–0.8 of length of largest. *Male flowers* with 10–13(–17) stamens, fused into carnose mass 2.8–3.9 mm diameter, with anthers borne in cavities; pollen hexacolpate. *Female flowers* with 18–37 free carpels, gynoeceum 2.8–3.8 mm diameter; ovaries 1.2–1.5 by 0.7–0.8 mm, length: width ratio 1.7–2.0; pseudostyle flat-subulate, without pseudostigma. *Fruit* pedicel short, 3–8 mm long; torus 30–50 mm long; berries 15–20 (possibly more), 6.7–8.5 by 6.6–8.2 mm, length: width ratio 0.9–1.2, berries borne on short stipes. *Seeds* (1 or) 2 per berry, ± discoid. — **Fig. 2.**

Distribution — *Malesia*: Java and Bali.

Habitat — Submontane to montane forests, 1200–2200 m altitude, although Koorders (l.c.) reports '*S. axillaris*' growing at altitudes of only 400 m.

Note — Although there are numerous reports of '*S. axillaris*' from Assam, Burma and Yunnan, Smith (l.c.) has shown that these refer to *S. propinqua* (Wall.) Baill. var. *intermedia* A.C. Sm. [= subsp. *intermedia* (A.C. Sm.) R.M.K. Saunders]. It is unclear whether the '*S. axillaris*' pollen described by N. Mitroiu [Acta Bot. Hort. Bucurest. '1969' (1970) 3–243] refers to *S. propinqua* subsp. *intermedia* or subsp. *axillaris* since no voucher specimens were cited, although the pollen structure appears to be identical nevertheless.

2. *Schisandra elongata* (Blume) Baill.

Schisandra elongata (Blume) Baill., Hist. Pl. 1 (1868) 148, f. 182; Backer, Schoolfl. Java (1911) 16; A.C. Sm., Sargentia 7 (1947) 120; Backer & Bakh. f., Fl. Java 1 (1963) 99; Steenis, Mountain Fl. Java (1972) t. 2.10. — *Sphaerostema elongatum* Blume, Bijdr. (1825) 23, '*elongata*'; Fl. Javae (1830) 17, t. 5. — *Sphaerostemma elongatum* Blume ex G. Don, Gen. Hist. Dichlam. Pl. 1 (1831) 101, '*elongata*'. — Type: Blume 1422 (L lecto), Java, Mt Burangrang.

Woody vines, monoecious. *Leaves* papyraceous, occasionally membranous, (3.5–)5–10 µm thick; lamina ovate, occasionally elliptic, (7–)9–12(–15) by (3.5–)4.5–7(–8.5) cm, length: width ratio (1.5–)1.7–2.1(–2.5); primary vein slightly impressed to impressed above, prominent below; secondary veins (3–)4–5 pairs, arcuate; base obtuse to truncate (acute in younger leaves), often short-decurrent; apex acuminate; margin denticulate, occasionally entire, 0–11(–15) teeth; petiole (13–)16–25(–46) mm long, (0.6–)

0.7–1.1(–1.5) mm diameter. *Flowers* borne axillary to leaves on young growth, solitary; pedicel (24–)30–40(–65) mm long, (0.2–)0.3–0.6(–0.7) mm diameter. *Perianth segments* 8–10; outermost perianth part ovate, 1.5–1.9(–3.2) by (1.5–)2.0–3.0 mm, length: width ratio (0.6–)0.9–1.2; innermost perianth part orbiculate, elliptic, ovate or obovate, (2.4–)4.2–5.2 by (2.2–)2.8–3.3 mm, length: width ratio (1.1–)1.3–2.0; largest perianth part ovate, 7.0–8.2 by (4.6–)6.9–8.4(–10.0) mm, length: width ratio 0.8–1.2(–1.5); outermost perianth part highly reduced to 0.2–0.4 of length of largest; innermost perianth part reduced to (0.3–)0.6–0.7 of length of largest. *Male flowers* with 27–30 stamens, filaments fused at the base only, androecium c. 3.5 mm diameter; pollen hexacolpate. *Female flowers* with 20–45 free carpels, gynoecium 3.0–3.4 mm diameter; ovaries 1.3–1.8 by 0.6–0.7(–0.8) mm, length: width ratio 2.0–3.0; pseudo-style round-subulate, without pseudostigma. *Fruit* pedicel elongated, 40–67 mm long; torus 31–75 mm long; berries 10–20 (possibly more), 6.8–8.6 by 4.5–6.2 mm, length: width ratio (1.1–)1.5–1.8, berries borne on short stipes 1.3–2.3 mm long. *Seeds* 2 per berry, discoid, 2.6–3.3 by 2.8–3.3 mm, length: width ratio 0.9–1.0.

Distribution — *Malesia*: endemic to Java.

Habitat — Submontane to montane forests, 1000–2000 m altitude.

Note — Although there are numerous reports of *S. elongata* from the Himalayas and Yunnan, Smith (l.c.) has shown that these refer to *S. neglecta* A.C. Sm. The '*S. elongata*' pollen described by J. Pragowski [World Pollen Spore Fl. 5 (1976) 1–32] represents *S. neglecta*.

EXCLUDED SPECIES

Kadsura blancoi Azaola in Blanco, Fl. Filip., ed. 2 (1845) 594; ed. 3 (1879) 118 = **Phytocrene blancoi** (Azaola) Merr., Philipp. J. Sc., Bot. 2 (1907) 432 (*Ilacinaeae*).

Kadsura pubescens Miq., Fl. Ned. Ind., Eerste bijv. (1861) 620 = **Actinidia miquelii** King, J. As. Soc. Beng. 59, ii (1890) 196 (*Actinidiaceae*).

Schizandra elongata Hook. f. & Thomson var. *marmorata* Hallier f., Bull. Herb. Boiss. 6 (1898) 214.

The taxonomic identity unclear, although not related to '*Schizandra marmorata*' or to '*Sphaerostema marmorata*' (= *Kadsura marmorata*) as suggested by Hallier, l.c.

LORANTHACEAE

(B.A. Barlow, Canberra, Australia)¹

Loranthaceae D. Don, Prod. Fl. Nepal (1825) 142; Miq., Fl. Ind. Bat. 1, 1 (1856) 807; Agardh, Theoria Syst. Pl. (1858) 117; Tiegh., Bull. Soc. Bot. France 43 (1896) 247; Barlow, Proc. Linn. Soc. New S Wales 89 (1964) 269; Backer & Bakh. f., Fl. Java 2 (1965) 67; Kuijt, Brittonia 20 (1969) 136–147; Barlow in Handb. Fl. Papua New Guinea 2 (1981) 206; in Fl. Austral. 22 (1984) 68; P. Royen, Alpine Fl. New Guinea 3 (1982) 2257; Wiens in Rev. Handb. Fl. Ceylon 6 (1987) 123; Barlow et al., The Golden Bough 11 (1989) 1–4 (Roy. Bot. Gard., Kew). — *Loranthaceae* subfam. *Loranthoideae* Engl., Nat. Pflanzenfam. 3, 1 (1889) 177; Tiegh., Bull. Soc. Bot. France 41 (1894) 138; Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 291; Verh. Akad. Wet. Amst. Afd. Natuurk. 29 (1933) 1–128. — Type genus: *Loranthus* L.

[For additional synonymy see Barlow, Proc. Linn. Soc. New S Wales 89 (1964) 269].

Perennial evergreen hemiparasites, usually aerial stem-parasitic shrubs, sometimes terrestrial root-parasitic shrubs or trees; attachment to the host (in aerial stem-parasites) by many haustoria produced on epicortical runners (especially in Malesia) or by a single complex woody primary haustorium. *Leaves* mostly opposite, less frequently alternate or verticillate, always simple; stipules absent. *Inflorescences* mostly axillary, less frequently terminal, internodal or borne on the epicortical runners; uniflorescence a simple dichasium (triad) or a single flower, these usually aggregated to racemose, umbellate or capitate compound inflorescences. *Flowers* dichlamydeous, mostly hermaphrodite, when unisexual plants mostly dioecious. *Calyx* a membranous limb at the apex of the ovary, without vascular bundles. *Corolla* choripetalous or gamopetalous, regular or somewhat zygomorphic, normally 4- to 6-merous, valvate. *Stamens* as many as and opposite the petals, epipetalous; anthers mostly basifixed, immobile and continuous with the filament, sometimes dorsifixed and then usually versatile, opening by longitudinal slits; pollen mostly trilobate, rarely triangular or spherical. *Ovary* ('calyx tube' of some authors) inferior; ovarian cavity with or without a central column (mamelon); ovules absent; sporogenous tissue massive, located in lobes of the mamelon or at the base of the ovarian cavity; style and stigma simple. *Fruit* mostly berry-like, with a single seed covered by a sticky layer which develops outside the vascular bundles.

1) With contributions by P. Baas (leaf anatomy), R.W.J.M. van der Ham (palynology), and L. van den Oever (wood anatomy). Drawings were mostly adapted from various earlier publications and redrawn at CSIRO Plant Industry Visual Resources Unit, Canberra, principally by Sandie McIntosh, with contributions by Sue Percival and Carl Davies. Photographs are from different sources as indicated.

DISTRIBUTION

About 65 genera and 950 species, predominantly tropical but well represented also in southern temperate regions; occurrence in the northern temperate zone is limited. In *Malesia* 23 genera and 193 species, distributed throughout the region; major centres of species richness are the Philippines, New Guinea and northern Borneo. For biogeography see below.

HABITAT

Mostly in tropical and warm temperate habitats; rare or absent in seasonally cold temperate situations. In *Malesia* distributed throughout the range of forest habitats from mangrove associations at sea level to the tropicalpine margins above 3000 m altitude. Common in all major forest types (everwet and seasonal, closed and open, humid and dry, primary and secondary, evergreen and deciduous); many species can flourish in disturbed or cleared areas and on exotic hosts.

An important element of habitat for *Loranthaceae* is the host; see below for discussion of host specificity.

ECOLOGY

Loranthaceae exhibit a suite of remarkable adaptations associated with the hemiparasitic habit, especially in the majority of the species which occur as aerial stem parasitic shrubs; for additional details see under morphology below.

Effective seed dispersal is by fruit-eating birds, and demonstrates close mutualism involving fruit and embryo structure, germination, and bird anatomy and behaviour (Docters van Leeuwen 1954; Reid 1989; Barlow & Schodde 1993). The ovoid seed, 5–12 mm long, is covered by a viscous layer rich in carbohydrates. The seed is removed from the fruit and swallowed whole, and passes through the short alimentary canal of the bird rapidly, commonly in 10–20 minutes. Although nutrients have been absorbed from the viscous layer, it is intact when the seed is voided. The most specialized bird dispersers, for example *Dicaeum* spp., perform specific movements when defecating, such that the voided seed is placed on the branch on which the bird is perched. The viscous layer cements the seed in place, and it germinates spontaneously, probably because it has been removed from an inhibiting environment within the wall of the fruit. These adaptations together greatly increase the likelihood that the seed will be dispersed to a suitable habitat on a tree branch. Instead of normal roots, the embryo radicle produces an haustorium which penetrates to the cambial layer of the host to take up water and nutrients from the xylem. See Fig. 1.

Host preference and specificity vary widely within the family. Most loranthos grow on dicotyledonous trees, but some utilize gymnosperms as occasional hosts, and a few species are specialized for growth on gymnosperms. In mixed forests with high tree species diversity the loranthos tend to have very low host specificity, occurring on a broad range of host species; this is the common situation in *Malesia*. In open woodlands with

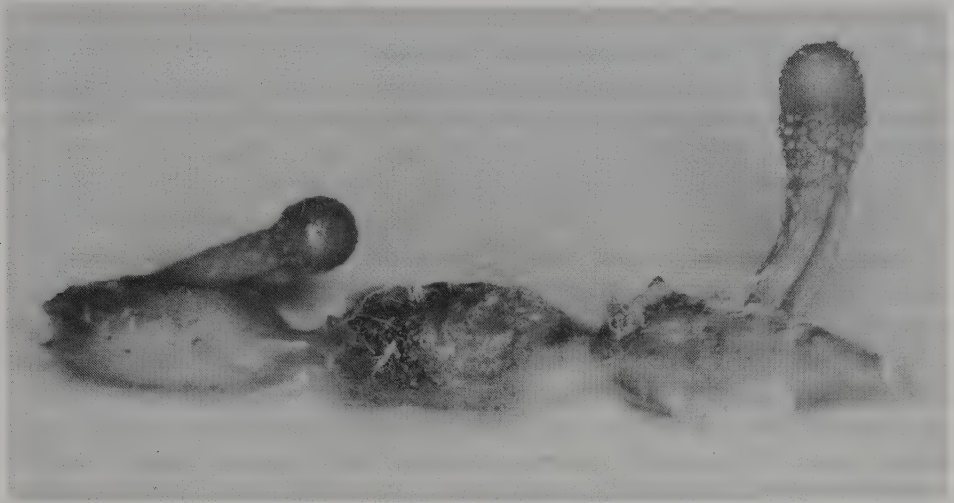


Fig. 1. Seedlings of unidentified loranthaceous seedling. Lombok. Photo E. Schmutz, with permission.

low tree species diversity and one or two dominant tree species, the loranth flora tends to be more closely adapted for growth on the common host, and therefore to show high host specificity. This situation is common in Australian woodlands, and occurs to a limited extent in the Malesian monsoon belt, especially in the Lesser Sunda Islands.

When host specificity is high the loranth species may sometimes show a visual resemblance to the preferred host (Barlow & Wiens 1977). By influencing the birds' search image, this may increase the likelihood of dispersal to the preferred host species. It may also confer some protection from herbivores. Because of the generally low host specificity of Malesian loranth this phenomenon is almost absent in Malesia, although the parasites of *Eucalyptus*, *Melaleuca* and *Pittosporum* in Timor and adjacent islands tend to resemble the host in leaf form. In rain forests any resemblance between the leaves of loranth and their hosts is probably convergence in response to habitat conditions rather than a genuine mimicry.

There are several pollination syndromes in the family. Bird pollination is most common and many genera, especially in Malesia, have tubular curved brightly coloured corollas with exserted stamens and nectar chambers at the base. In Malesia the pollinators are commonly sunbirds to the west of Charles's Line and honeyeaters to the east. Beyond Malesia bird pollination may include explosive mechanisms, especially in Africa. Insect pollination also occurs, and is indicated in species with relatively small spreading choripetalous corollas or short bell-like tubular corollas which are often pale-coloured. Insect pollination is probably the primitive state for the family (see below), and in Malesia this may be represented in *Cecarria*. In other genera such as *Amyema* and *Dendrophthoe* insect pollination may be a secondary development. In some Malesian genera, notably *Macrosolen* and *Trithecanthera*, slender tubular corollas may reach 150 mm in

length, and may be pollinated by moths. Beyond Malesia, corolla lengths up to 250 mm occur, notably in the South American genus *Aetanthus*.

References: Barlow, B. A. & R. Schodde, *Beaufortia* 43 (1993) 124–129. — Barlow, B. A. & D. Wiens, *Evolution* 31 (1977) 69–84. — Docters van Leeuwen, W. M., *Beaufortia* 4 (1954) 105–207. — Reid, N., *Ecology* 70 (1989) 137–145.

MORPHOLOGY

Haustorial system — The haustorial system in *Loranthaceae* shows considerable diversity. The primitive state, found in a few genera, is terrestrial root-parasitism with no primary haustorium, which is common in the related families *Olacaceae* and *Santalaceae* (Calder & Bernhardt 1983). Among aerial *Loranthaceae* the apparently most primitive haustorial system involves basal epicortical roots (referred to as ‘runners’), which grow in vine-like fashion along the host stems, producing haustoria at regular intervals. They can produce new leafy shoots and sometimes inflorescences along their length. The epicortical runners may represent an early stage in evolution from terrestrial root-parasitism to aerial stem-parasitism, in which root-like structures producing numerous haustoria are still present (Hamilton & Barlow 1963). Species with epicortical runners are most common in humid tropical forests, and in Malesia the great majority of loranthids exhibit this character. The more advanced haustorial systems are those in which epicortical runners are not produced, and only the primary haustorium developed from the embryo is present. This may be very complex, especially in internal structure; some produce long strands which extend for metres inside the host, either in the cambial zone or in the cortex (Hamilton & Barlow 1963). In Malesia such haustoria are rare, generally being found in species with close phyletic links to Australia, where such haustoria are common. Haustoria produced from stem-borne roots, as in the neotropical genus *Struthanthus*, probably also represent a derived state, but do not occur in any Malesian species.

The haustoria in most mistletoe species are xylem-tapping, although some species also tap the phloem and therefore have easier access to host photosynthate. Xylem-tapping mistletoes nevertheless divert and concentrate nutrients such as nitrogen and phosphorus from the host’s sap. On average, about 15% of the total carbon gain of xylem-tapping mistletoes is from photosynthate diverted from the xylem stream of the host (Moore 1994; Marshall et al. 1994).

Inflorescences — There are several parallel trends in inflorescence structure in *Loranthaceae*. The most primitive inflorescences appear to be simple cymes, and a common inflorescence unit widespread in the family is a simple dichasium (triad). The triads are often aggregated into larger compound inflorescences, which are usually racemose or umbellate (Fig. 5, 8, 18). A secondary trend in inflorescence evolution appears to be reduction from this compound state, and simple racemes or umbels, for example, are probably derived through reduction of triads to single flowers. This is clearly evident in *Macrosolen*, where each flower in the raceme is subtended by three bracts (Fig. 36–38). In Malesia reduction in inflorescence structure reaches its extreme in some species of *Amyema* and in *Sogerianthe*, where the inflorescence is a single flower but its articulate pedicel is evidence of its derivation (Fig. 6, 42).

Another trend in inflorescence evolution is the contraction of the flowers into heads, often subtended by enlarged bracts which form an involucre. Such inflorescences are more common in loranth in Malesia than in any other region, and parallel evolution of capitate inflorescences has occurred in a number of lineages. The basic racemose or umbellate nature of the inflorescence is still usually evident, as well as the presence of triads or single flowers as the basic inflorescence unit. In many capitate inflorescences the young flowers are tightly enclosed during development, possibly for protection (Fig. 31, 32, 40, 44). However, at anthesis the flowers may be exerted from the involucre, which is often brightly coloured and probably contributes to the presentation of the flowers to pollinators. This interpretation of inflorescence evolution agrees in its broadest principles with the conclusions of Kuijt (1981), but differs in many details.

Flowers — Whilst the external form of the flowers does not appear exceptional, there are some very unusual features of ovary structure and embryology (Maheshwari et al. 1957; Johri & Bhatnagar 1960). There are no normal ovules. In many species there is a central mound or column, the mamelon, which occupies most of the ovarian cavity, and which may be homologous with an axile placenta. In some cases the base of the mamelon is lobed, and these lobes may be homologous with ovules. Bands of tissue radiating between the lobes to the ovary wall may form 3 or 4 obscure cells in the ovarian cavity, and are possibly homologous with septa. In other cases the mamelon is simple or completely absent, and the ovarian cavity is hardly more than a small dilation of the base of the stylar canal. The sporogenous tissue is massive, located either in 3 to 4 blocks in the mamelon lobes or in a single block at the base of the ovarian cavity. These structures may represent progressive reduction of a syncarpous ovary, and the extreme of the reduction sequence, for example in *Amyema*, is an almost completely undifferentiated ovary with a single group of sporogenous cells at the base of the stylar canal. There are several embryo sacs which elongate up the stylar canal to various levels, so that fertilization occurs in the style, sometimes close to the base of the stigma (*Helixanthera*, *Dendrophthoe*). Rapid development of a long suspensor pushes the proembryo down into the ovary before the style is shed. Normally only one embryo develops in the seed, and the viscous layer develops from a zone in the ovary wall outside the vascular bundles. These features of embryology are so exceptional in angiosperms that Van Tieghem (1896) treated loranth and related groups as a subclass of the angiosperms with rank equivalent to the monocotyledons and dicotyledons.

Seeds and seedlings — Seed and seedling features may provide useful diagnostic characters at a tribal or subfamilial level in *Loranthaceae*. The seeds are primarily endospermic, although in the neotropical genus *Psittacanthus* the endosperm appears to be entirely absorbed in mature seeds. The embryo is normally green. In many genera the cotyledons emerge as the first photosynthetic leaves after germination. In others the slender cotyledons remain in the endospermic seed, elongating to push out the plumule, which produces the first leafy shoot. These two basic germination patterns are generally correlated with other characters of taxonomic importance at higher ranks, especially basic chromosome number and ovary structure.

References: Calder, D.M. & P. Bernhardt, *The Biology of Mistletoes* (1983). — Hamilton, S.G. & B.A. Barlow, *Proc. Linn. Soc. New S Wales* 88 (1963) 74–90 (haustorial structure). — Johri, B.M. & S.P. Bhatnagar, *Proc. Nat. Inst. Sc. India* 26B (1960) 199–220 (embryology). — Kuijt, J., *Blumea* 27 (1981) 1–73 (inflorescence structure). — Maheshwari, P., B.M. Johri & S.N. Dixit, *J. Madras Univ.* 27 (1957) 121–136 (floral morphology, embryology). — Marshall, J.D., J.R. Ehleringer, E.-D. Schulze & G. Farquhar, *Funct. Ecol.* 8 (1994) 237–241 (nutrient uptake). — Moore, P.D., *Nature* 369 (1994) 277–278 (nutrient uptake). — Van Tieghem, P., *Bull. Soc. Bot. France* 43 (1896) 241–256 (classification).

VEGETATIVE ANATOMY

(P. Baas, leaf anatomy & L. van den Oever, wood anatomy)

Leaf anatomy — Our knowledge of the leaf anatomy of the *Loranthaceae* is mainly based on studies of taxa outside Malesia. Metcalfe & Chalk (1950) recorded an interesting leaf anatomical diversity for the family as a whole. The indumentum, when present, tends to be complex and includes candelabra and stellate hairs (Engler & Krause 1935; Uphof et al. 1962). The lamina is dorsiventral or isobilateral, and amphistomatic in the latter case. Stomata paracytic. Groups of silicified cells (also typical of many genera in the related families of the *Viscaceae* and *Oleaceae*, cf. Baas et al. 1982) occur in the mesophyll of some genera. Sclereids, present in some taxa, including *Dendrophthoe* spp. (Rao & Malaviya 1962), often including crystals. Vascular bundles supported by arcs of sclerenchyma or collenchyma. Crystals solitary and/or clustered. Detailed study will almost certainly yield information of taxonomic interest.

Wood anatomy — The wood anatomy of Malesian *Loranthaceae* is very poorly known. The account below is based on original observations on a few Southeast Asian species (*Dendrophthoe curvata* from Sulawesi, *D. neelgherrensis* from Sri Lanka, *Helixanthera parasitica* from Sulawesi, and *Tolyphanthus gardneri* from Sri Lanka) and some general information from the literature in Metcalfe & Chalk (1950) and Patel (1991). The quantitative data are restricted to the original observations, and may be very different for temperate species or stems and branches of smaller diameter.

Growth rings absent to distinct. Vessels diffuse, 25–48/mm², solitary and in radial multiples or small clusters, tangential diameter up to 60–80 µm, vessel member length 420–780 µm in *Dendrophthoe curvata*, in the other specimens only up to 100 µm. Perforations simple. Intervessel pits small, alternate, vessel-ray and vessel-parenchyma pits alternate, similar in shape and size to intervessel pits, occasionally large and simple. Vessel elements storied structure together with axial parenchyma. Ground tissue composed of relatively thin-walled fibre-tracheids with distinctly bordered pits in radial and tangential walls (in *D. curvata* mainly confined to the radial walls).

Parenchyma predominantly apotracheal, diffuse, partly scanty paratracheal, in strands of 2–5 cells.

Rays mostly multiseriate (up to 12 cells wide) and weakly heterocellular to homocellular; in *D. curvata* distinctly heterocellular and 1–3-seriate.

Crystals solitary, infrequent in non-chambered ray or axial parenchyma cells.

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POLLEN MORPHOLOGY

(R. W. J. M. van der Ham)

Only the smaller, neotropical part of the family *Loranthaceae* is palynologically well-known. Feuer & Kuijt (1979, 1980, 1985) described the pollen of all 16 American genera listed by Barlow et al. (1989), nearly every time including scanning as well as transmission electron micrographs. A few relatives from Australia and New Zealand (*Atkinsonia*, *Nuytsia*, *Tupeia*) were treated similarly (Feuer & Kuijt 1978, 1980), but the pollen of most other paleotropical genera is unknown or described on the basis of limited data only. Danser (1933) and Barlow (1966, 1974) used pollen grain shape as a character in their generic keys. More detailed accounts of a few taxa were later published in several regional studies: Africa: Bonnefille & Rioulet (1980), El Ghazali (1993); Madagascar: Muller et al. (1989); China: Liu & Qiu (1993); New Zealand: Moar (1993). The Chinese study contains species of several widespread genera occurring also in Malesia (*Dendrophthoe*, *Elytranthe*, *Helixanthera*, *Loranthus*, *Macrosolen*, *Scurrula*, *Taxillus*). Data of the Papuasian genera in Malesia are nearly absent.

Pollen grains of most *Loranthaceae* are relatively flat, triangular with concave (pollen 'trilobate') or sometimes straight to slightly convex sides, and 3-aperturate or rarely almost spheroidal and 4- or 5-aperturate (*Ixocactus*, *Tupeia*). The largest diameter (equatorial plane) is between 20 and 99 µm. The apertures are usually simple (ectoapertures without endoapertures). Compound apertures with more or less distinct endoapertures were observed in a few neotropical genera, and are considered as derived conditions (Feuer & Kuijt 1985). The spheroidal, inaperturate pollen of *Atkinsonia* is unique in the family. The aperture system found in most *Loranthaceae* is syncolpate, although the colpi are often less distinct or even absent at the poles (pollen more or less colpate) and/or at the equatorial plane (pollen diplodemisyncolpate). The germinative parts of the colpi seem to be about halfway between each pole and the equator (6 per grain), and are indicated by a thin, invaginating or teared up colpus membrane. In some genera the germinative function is still more clearly confined, the apertures being reduced to very short colpi or pori enclosed and connected by thick exine zones (*Dendropemon*, *Oryctanthus*, *Phthirusa*). The harmomegathic function in *Loranthaceae* pollen seems to be transferred from the apertures to the mesocolpia. As far as known parasyncolpate apertures are restricted to a few neotropical genera. Strongly heteropolar (shape, apertures) pollen is known from the African genus *Plicosepalus*. The exine is 3-layered (tectum, infratectum, nexine), at least in the electron microscope. An endexine is usually found only in apertural regions. The infratectum is thin, and granular, columellate or intermediate. Or-

namentation in *Loranthaceae* is psilate, scabrate, verrucate or sometimes echinate, with or without small perforations. Finely rugulate pollen occurs in Brazilian *Struthanthus*. The exine zones along the colpi ('margines') are often distinct by a deviating ornamentation compared with the mesocolpia: psilate to transversely striate vs scabrate to verrucate.

Some genera are palynologically very diverse (see also Castro & Telleria 1995), and pollen morphology has been useful in establishing intra- and intergeneric relationships (Feuer & Kuyt l.c.). However, due to the lack of data from many of the Old World genera a subdivision of the family is unfeasible yet. More or less typical loranthaceous pollen is shared by relatively primitive (*Desmaria*, *Gaiadendron*, *Nuytsia*) and advanced (*Ligaria*, *Psittacanthus*, *Tristerix*) genera (sequence according to Barlow et al. 1989). Deviating morphologies seem to dominate in relatively primitive groups: *Atkinsonia*, *Tupeia*, *Ileostylus*, *Ixocactus*, *Dendropemon*, *Phthirusa*, *Oryctanthus*. The pollen characters of *Ixocactus* and *Tupeia* indicate relationships to the *Eremolepidaceae* and/or *Viscaceae* (Feuer & Kuijt 1978, 1985).

Possibly, the differences between trilobate *Loranthaceae* pollen and the spheroidal pollen of the *Viscaceae* and *Eremolepidaceae* are connected with pollination: largely by birds in the former and by insects at least in the *Viscaceae*. Bernhardt & Calder (1981) depict (SEM) a strongly lobate pollen grain of *Amyema* attached to/lodged in the parallel feather barbles of a honey eater.

Fossil pollen that can be attributed to the *Loranthaceae* is known from Europe, America, India, Indian Ocean (Ninetyeast Ridge), Borneo, Australia and New Zealand, and ranges from the early Paleocene onwards (Muller 1981; Taylor 1990). It has been described as *Gothanipollis*, *Aethanthus*, *Amylotheca*, and compared to the pollen of several extant genera (*Amylotheca* type, *Loranthus elegans* type). Taylor (1989) illustrated (LM and SEM) *Gothanipollis cockfieldensis* from the Eocene of Tennessee, which is much like the pollen of *Tripodanthus flagellaris*. Thanikaimoni et al. (1984) compare *Loranthipites elegans* from the Miocene of India with the pollen of *Dendrophthoe falcata*. *Tricolpites simatus* described from the Eocene of southern Australia is probably also a fossil loranth (Macphail et al. 1993). According to Jarzen (1977) isopolar forms of the fossil genus *Aquilapollenites* (Traverse 1988: late Cretaceous to Eocene) bear a close morphological and probably genetic relationship with *Loranthaceae* pollen. However, *Aquilapollenites* is an exclusively Laurasian group, while the present distribution patterns of the more primitive extant *Loranthaceae* suggest a Gondwanan origin. The inception of the undoubtedly loranthaceous *Gothanipollis* is linked with the expansion of *Nothofagus*, attesting to the age of the *Loranthaceae* in the southern lands. The fossil pollen record shows the presence of the family in Tasmania from the early Eocene throughout the Tertiary until the ?late Pleistocene (Macphail et al. 1993), even though mistletoes (and mistletoe birds) are now absent there.

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CHROMOSOMES

Chromosomal characters have made a significant contribution to taxonomic and phylogenetic knowledge of the family (Barlow & Wiens 1971; Martin & Barlow 1984). The primary basic chromosome number is $x = 12$, and the other basic numbers of $x = 11$, 10, 9 and 8 indicate progressive dysploid reduction. Polyploidy is virtually absent, but there is a general trend towards increase in chromosome size, and the largest chromosomes in the family are equal to any in the plant kingdom. There is considerable genomic stability, with particular chromosome numbers and sizes being constant for entire suites of related genera, and cytogeographic data are therefore phylogenetically useful. In Malesia there are lineages with $x = 12$ and $x = 9$, with different geographic histories; see discussion under biogeography below.

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PHYTOCHEMISTRY AND CHEMOTAXONOMY²

Much of the phytochemical study of mistletoes has been undertaken at a time when *Loranthaceae* and *Viscaceae* were treated as a single family *Loranthaceae* sens. lat. Furthermore many of the studies have involved comparative work in several genera of both families, identifying similarities and differences between the groups then considered subfamilies. For this reason it is appropriate to consider the phytochemistry of the two families together, to identify the contribution of chemotaxonomy to the current treatment of the two families. Chemical data are not available for a third segregate family, *Eremolepidaceae*, and the status of this family is not considered further.

The chemical data presently available, although limited, allow some general observations on the taxonomic significance of metabolism and storage of primary and secondary plant products in stems, leaves, fruits and seeds of mistletoes, and their two major component groups, *Loranthaceae* and *Viscaceae*.

Apart from the considerable attention given to the traditional European mistletoe, *Viscum album*, phytochemical investigations of mistletoes are relatively few. The phyto-

2) This section has been written almost entirely on the basis of information, analysis and conclusions contributed by R. Hegnauer, Leiden. Without his valuable input, this section could not have been written, and it is most gratefully acknowledged.

chemistry of *Loranthaceae* s.l. and its possible taxonomic implications were treated by Hegnauer (1966, 1989, where many additional phytochemical references are given). Many aspects of the biology of semiparasitic *Santalales*, especially of *Loranthaceae* and *Viscaceae*, were reviewed in a work edited by Calder & Bernhardt (1983). A series of International Symposia on Parasitic Flowering Plants (e.g., Weber & Forstreuter 1987) has also fostered contributions to phytochemical knowledge. Becker and Schmoll (1986) published a valuable ethnobotanical monograph of European *Viscum album*, and Kanner (1939) of mistletoes generally, of relevance for all students of mistletoes.

Phytochemistry of parasites — Because all mistletoes are parasitic (most hemiparasitic, some holoparasitic) it is possible that chemical compounds isolated from a particular mistletoe are not metabolites of the parasite, but were in fact derived from its host plant. Comparative analyses of host plants and their parasites are essential for establishing definitely the site of synthesis, especially of easily transportable hydrophilic mistletoe constituents. It has been shown that a number of secondary metabolites such as tropane alkaloids in *Duboisia*, cardenolides in *Nerium* and tutin and related toxic terpenoid hydroxylactones in *Coriaria* can pass in rather large amounts from hosts into their parasites. Some carbohydrates and carbohydrate-like compounds such as mannitol and certain cyclitols (e.g. quercitol) isolated from mistletoes may have their origin in the host plant (Plouvier 1953). Richter and Popp (1987) showed that whilst pinitol, quebrachitol and *chiro*-inositol are characteristic of *Viscum album*, sorbitol and *scyllo*-inositol are only present when they occur in the host. Studies in *Viscum album* by Urech (1987) also suggest that arginine is taken up from the host. Room (1971) showed that *Tapinanthus bangwensis* can act as a sink for products of photosynthesis manufactured by cocoa, and Kanner (1939) reported that mistletoe growing on coffee may have almost as much caffeine in its leaves as the host. Studies in *Amyema* by Hall et al. (1987a, b) suggest that cytokinins are acquired from the host, although they may be converted in the parasite to other forms. Whilst most mistletoes are xylem-tapping, some are also phloem-tapping (see under morphology and anatomy); this may explain the diversity of substances which appear to be acquired from the hosts.

On the other hand extensive comparative studies of species of *Loranthaceae* and some of their host plants in Africa, eastern Asia, Australia and America, and of *Viscum album* and many of its hosts in Europe (Plouvier 1953), have clearly established that mistletoes are largely independent from their hosts with respect to patterns of most of their low-molecular phenolic constituents, biogenic amines or protoalkaloids and methylated cyclitols. Similarly, mistletoes appear to be characterized by the presence of relatively large amounts of free proline and/or hydroxyproline. In other cases there appear to be consistent phytochemical differences between *Loranthaceae* and *Viscaceae*. By making allowance for the parasitic habit of the plants, it therefore seems possible to reach some preliminary but nevertheless taxonomically meaningful conclusions.

Phytochemical features in common to Loranthaceae and Viscaceae — Several biochemical similarities between *Loranthaceae* and *Viscaceae*, and often other members of *Santal-*

ales, have been reported. In some cases these may relate to particular adaptations, such as the presence of a viscous layer in fruits of *Loranthaceae* and *Viscaceae*. Features shared by *Loranthaceae* and *Viscaceae* include:

a) Presence of much free proline (or) hydroxyproline in fruits, leaves, stems and haustoria.

b) Presence of acetylenic fatty acids in the lipids in vegetative parts.

c) Frequently, presence of large amounts of pentacyclic triterpenes, alkanols, alkanes, fatty acids and esters in the lipids of stems, leaves and fruits. These are probably constituents of cuticular waxes. The following triterpenes are known from mistletoes: lupeol, 7-hydroxy lupeol (loranthin), 7,15-dihydroxy lupeol, betulin, betulinic acid, β -amyrin and oleanolic acid. Sometimes the 3-hydroxyle of these triterpenoids is acylated by acetic acid or by fatty acids. However saponins (glycosides of triterpenoids) have not yet been isolated.

d) Production and storage of appreciable amounts of tyramine or phenylethylamine or related biogenic amines or betaines.

e) Storage in all parts of these plants of rather large amounts of *myo*-inositol and *chiro*-inositols.

f) An extremely variable flavonoid mechanism. Chalcones, flavanones, flavanonols, flavones, C-glycoflavones, flavonols (including many methyl ethers of quercetin), flavan-3-ols (catechins) and 3-deoxycatechins (the viscutins of *Viscum tuberculatum*) have been isolated from one or several taxa of this alliance. Flavonoid metabolites with a trihydroxylated B-ring seem to be rare in mistletoes, but were shown to be present in many *Arceuthobium* species (Crawford & Hawksworth 1979: glycosides of myricetin; Bate-Smith 1962: prodelphinidins in *A. oxycedri*). Flavonoids are often accompanied by phenolic benzoic and cinnamic acids which generally are present as esters, and by small amounts of glycosides of coniferyl alcohol, syringenin and the bifuranoid lignan syringaresinol.

g) A tendency to deposit large amounts of silica in cell groups of the mesophyll (Solereder 1899, 1908). In numerous studies published between 1895 and 1907, Van Tieghem recorded the occurrence of these deposits, and frequently used it to support his distinction of genera. This rather surprising feature in a group of hemiparasitic plants has subsequently been given little attention by botanists. It was not treated at all in the review by Calder & Bernhardt (1983), and no additional information was presented by Metcalfe & Chalk (1950). Deposition of silica occurs in cells of many members of the *Santalales*, and it seems possible that a careful study of SiO_2 -accumulation in leaves and stems of mistletoes may yet contribute to classification in this taxonomically difficult alliance.

Phytochemical differences between Loranthaceae and Viscaceae — A number of metabolic patterns and/or individual constituents appear to be restricted to or occur predominantly in either *Loranthaceae* or *Viscaceae*. These differences have sometimes been used to support distinction of these two taxa at family rank. The status of such chemical markers may be summarized as follows:

a) The viscous layer in fruits of *Loranthus europaeus* and of various South American and African *Loranthaceae* contains large amounts of rubber, which makes such fruits suitable for the preparation of birdlime (Riley 1963; Uphof 1968). Accumulation of rubber seems to be lacking in *Viscaceae*; reports in older literature that birdlime was produced from berries of *Viscum album* were probably the result of confusion with *Loranthus europaeus*. Reliable data suggest that this distinction holds for *Loranthaceae*, which produce rubber-rich fruits, and *Viscaceae*, which have rubber-poor or rubber-lacking fruits.

b) In addition to *chiro*- and *myo*-inositol, *Viscum album* also produces and stores methyl ethers of cyclitols, i.e. pinitol, quebrachitol, 1-O-methyl-*muco*-inositol and viscumitol (1,2-di-O-methyl-*muco*-inositol). These methylated cyclitols seem to be restricted to *Viscaceae*, having been detected so far in *Arceuthobium* and five species of *Viscum*. *Loranthaceae* appear not to possess cyclitol-methylating enzymes and also to lack cyclitol-epimerizing enzymes [(+)-*chiro*-inositol \rightarrow *muco*-inositol, resp. D-pinitol \rightarrow 1-O-methyl-*muco*-inositol]. In particular, methylated cyclitols and *muco*-inositol were not detected in *Dendrophthoe falcata*, *Macrosolen cochinchinensis*, *Loranthus europaeus*, *Scurrula parasitica* or *Taxillus cuneatus* (Richter et al. 1990; Richter 1992).

c) Most *Viscaceae* are tannin-poor plants, whilst many species of *Loranthaceae* have been reported to contain rather large amounts of tannins. For a long time plant anatomists noted the presence of tannin-containing idioblasts in ordinary parenchymatic cells in *Loranthaceae*; according to Metcalfe and Chalk (1950) "tanniferous cells (are) present in parenchymatous tissues, particularly of *Loranthoideae*" (= *Loranthaceae* s. str.). *Loranthaceous* tannins are mainly of the condensed type, based on catechins and oligomeric proanthocyanidins. Condensed tannins may be accompanied in some taxa by gallo- and ellagitannins. In particular, ellagic acid was detected by Bate-Smith (1962) in leaf-hydrolysates of *Nuytsia floribunda*, and taxillusin of *Taxillus kaempferi* is a monogallate of (+)-taxifolin-3-glucoside. Recently leaves of this taxon, growing on *Pinus thunbergii*, yielded taxillusin and three 3-monoglycosides of quercetin, i.e. avicularin, hyperin and quercitrin and (+)-catechin and the dimorphic procyanidins B-1 and B-3 were isolated from its stems (Konishi et al. 1996). Tilney and Lubke (1974) observed complex patterns of phenolic compounds in leaves and stems of *Erianthemum dregei*, *Tapinanthus minor*, *T. oleaefolius*, *T. rubromarginatus* and *T. zeyheri* (*Loranthaceae*) and *Viscum capense*, *V. combreticolum*, *V. obovatum*, *V. obscurum*, *V. rotundifolium* and *V. verrucosum* of South Africa. Two constituents were identified positively; catechin, a building stone of condensed tannins, detectable in leaves and stems of all *Loranthaceae* sampled, and chlorogenic acid, an ester of caffeic acid, present in all *Viscum* species sampled. The latter compound seemed to be lacking in all *Loranthaceae* samples. (+)-Catechin was isolated from the South American *Loranthaceae* *Tripodanthus flagellaris* and *Ligaria cuneifolia*.

Other taxa may have a polyphenolic metabolism which is somewhat intermediate between those typical of *Loranthaceae* and those typical of *Viscaceae*. *Arceuthobium* (*Viscaceae*) seems to have its own polyphenolic pattern; it has many flavonoids with a trihydroxylated B-ring (several glycosides of myricetin) in twigs and leaves of all 36 investigated species (Crawford & Hawksworth 1979) and it seems also to be rich in pro-

delphinidins, at least in *Arceuthobium oxycedri* (Bate-Smith 1962). Cambie et al. (1961) screened for alkaloids, saponins and proanthocyanidins in seven New Zealand mistletoes, including one belonging to *Viscaceae* (*Korthalsella salicornioides*) and six belonging to *Loranthaceae* (*Trilepidea adamsii*, *Peraxilla colensoi*, *P. tetrapetala*, *Alepis flavida*, *Ileostylus micranthus* and *Tupeia antarctica*). Saponins were lacking in all and alkaloids were present only in *Peraxilla tetrapetala*.

Proanthocyanidins were absent from leaves, bark and wood of *Tupeia antarctica* (a dioecious species which has been referred to *Viscaceae* by some authors), but present in all six other species. The proanthocyanidins of *Korthalsella* appear to resemble those of *Arceuthobium*. The differences in phenolic patterns between *Loranthaceae* and *Viscaceae* are thus not absolute.

d) *Loranthaceae* and *Viscaceae* differ in their content of toxic glycoproteins (lectins) and polypeptides. Toxic polypeptides (viscotoxins, including phoratoxin) which are highly toxic to mice after intraperitoneal injection, are restricted to *Viscaceae* (five genera and 21 species tested; presence of viscotoxins demonstrated for all five genera and nine of the species). None of the four genera and 26 species of *Loranthaceae* contained viscotoxin-like polypeptides. The viscotoxins and lectins of *Viscum* were clearly arranged by Becker (in Becker & Schmoll 1986), and *Viscum* lectins were comprehensively reviewed by Luther (1982) and by Goldstein & Poretz (1986). Work with viscotoxin-like basic polypeptides containing 46 amino acid residues was summarized by Samuelsson (1966, 1969, 1972) and by Ramshaw (1982).

Chemotaxonomy: summary — Several plant constituents common to *Loranthaceae* and *Viscaceae* occur more generally in *Santalales*, and may thus provide some support for the higher level classification of families within this order. However, there are other phytochemical features which may add support to the distinction of *Loranthaceae* and *Viscaceae*, already strongly indicated by morphological, anatomical, karyological and other data. In *Loranthaceae* intensive rubber synthesis in fruits and accumulation of condensed tannins (oligo- to polymeric proanthocyanidins) and of their monomers (catechins) occur frequently, whilst presence of viscotoxin-like basic polypeptides and synthesis and accumulation of methylated cyclitols are rather characteristic of *Viscaceae*.

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USES

Mistletoes, including *Loranthaceae*, feature prominently in folk legend and medicine (Kanner 1939; Barlow 1987). Superstitions about mistletoe are widespread in many human cultures, and involve numerous species. In most cases mistletoes were regarded as a good omen, providing protection from misfortune, injury, crop failure or evil spirits, or good luck in finding wealth or fertility. They have been widely used medicinally, to treat a broad range of afflictions, through both internal and external application. In the related family *Viscaceae* some of these uses appear to be based on genuine medicinal properties (antispasmodic, diuretic, antihæmorrhagic, muscle toning, lowering blood pressure), but *Loranthaceae* do not appear to have these properties. The widespread prominence of mistletoe in legend and medicine is probably due to its growth habit. When growing on trees of ritual or utilitarian importance (see Fig. 2), it may have been regarded as the ‘heart’ of the tree, important for its survival.

References: Barlow, B. A., *Biologist* 34 (1987) 261–269. — Kanner, L., *Bull. Hist. Med.* 7 (1939) 875–936.

TAXONOMY

Until relatively recently the family *Loranthaceae* has been treated in a broader sense. It was traditionally divided into two subfamilies, *Loranthoideae* and *Viscoideae*, the latter including genera now placed in *Viscaceae* and *Eremolepidaceae*. There are substantial differences between *Loranthaceae* sens. str. and *Viscaceae* in flower and fruit development and structure, summarized by Barlow (1964). The brief diagnostic key to the two families presented at the end of this section covers all Malesian taxa. *Loranthaceae* and *Viscaceae* may not be directly related; the former is possibly derived from root parasitic *Olacaceae*, whilst the latter is probably close to and derived from aerial stem-parasitic *Santalaceae* (Kuijt 1969).

At generic level, the taxonomic history of *Loranthaceae* sens. str. (= *Loranthoideae*) has been turbulent. Originally hundreds of species were assigned to a single genus *Loranthus*, which was therefore cosmopolitan and very heterogeneous. Many segregate genera had been recognized early in the 19th century (but subsumed in *Loranthus* by other authors), and in this respect the work of Blume was notable for Malesia, as he recognized several genera now widely accepted (*Dendrophthoe*, *Elytranthe*, *Lepeostegeres*, *Loxanthera*, *Macrosolen*). Engler (1889) recognized 10 genera, but still retained a very large and diverse genus *Loranthus*. Between 1894 and 1902 Van Tieghem revised the loranthids,



Fig. 2. *Dendrophthoe pentandra* (L.) Miq. and/or *D. praelonga* (Blume) Miq. on leafless kapok trees *Ceiba pentandra* (L.) Gaertn., cultivated in Java (?). Photo J.C. van der Meer Mohr.

recognizing many new diagnostic characters, and distinguishing about 100 genera. However, Van Tieghem's approach was somewhat mechanical, and he used diagnostic characters of doubtful value as generic determinants repeatedly in different groups. Between 1929 and 1933 Danser reviewed and rationalized Van Tieghem's work, and recognized c. 65 genera, including a few he circumscribed himself. The generic classification of the family now generally accepted is little different from that of Danser (1929, 1933); for summary see the outline by Kuijt in Barlow et al. (1989). It is fortunate that Danser's special interest was in Malesian *Loranthaceae* and *Viscaceae*, as his work has provided a critical and substantial base for the present treatment.

At the species level loranths have presented much taxonomic difficulty. Many species show considerable variability, and there is evidence of introgression in many taxa. Numerous segregate taxa have been recognized where narrow species concepts have been applied, and have resulted in unsatisfactory treatments from both practical taxonomic and biogeographic viewpoints. For Malesia numerous names have been placed in synonymy, both by Danser (1931, 1935) and Barlow (1974, 1992, 1993). For further discussion see Barlow (1992: 297).

Phylogenetic analysis of *Loranthaceae* is aided by suites of character states in which polarity is clear and correlations strong. These include karyological and embryological

data, morphological data from haustorial, inflorescence and floral structures, pollination syndromes and geographic relationships (see above). For details see Barlow (1983). The phylogeny of the family is strongly reflected in its biogeography (see below).

Subsequent to the recognition of *Loranthaceae* and *Viscaceae* as distinct families, there has been only limited attention to the classification of genera into infrafamilial groups. Kuijt, in Barlow et al. (1989), recognized a number of informal groups of genera in a provisional treatment not yet formalized. In this treatment the Malesian genera are grouped as follows.

Group "21–30": *Amylothea*, *Cyne*, *Decaisnina*, *Elytranthe*, *Lampas*, *Lepidaria*, *Lepeostegeres*, *Loxanthera*, *Macrosolen*, *Thaumasianthes* (the last transferred from Group "31–39").

Group "31–39": *Amyema*, *Cecarria*, *Dactyliophora*, *Distrianthes*, *Papuanthes*, *Sogerianthe*.

Group "40–70": *Barathranthus*, *Dendrophthoe*, *Helixanthera*, *Loranthus*, *Scurrula*, *Taxillus*, *Trithecanthera*.

Group "21–30" corresponds with subtribe *Elytranthinae* Engl., recognized by Danser (1933), distinguished by cotyledons emerging from the seeds and expanding during germination, and by a basic chromosome number of $x = 12$. Groups "31–39" and "40–70" together correspond with subtribe *Hypheatinae* Danser as accepted by Danser (1933). This subtribe is distinguished by cotyledons remaining embedded in endosperm in the seeds during germination, and by a basic chromosome number of $x = 9$. Groups "31–39" and "40–70" differ in basic inflorescence structures (although obscured by inflorescence evolution in each Group), and generally in chromosome size. Group "31–39" is Australian/Papuan in origin, whilst Group "40–70" is African/Asian. See also the discussion on plant geography below.

KEY TO THE FAMILIES

- 1a. Perianth monochlamydeous, with tepals mostly less than 2 mm long; flowers unisexual, with male and female flowers usually in the same inflorescence; pollen spherical; fruit with the viscous layer inside the vascular bundles; embryo suspensor very short or absent **Viscaceae** (p. 403)
- b. Perianth dichlamydeous, with the calyx reduced to a limb at the apex of the ovary and the corolla (2.5–)10–150 mm long; flowers mostly bisexual, rarely functionally unisexual and then with vestigial organs of the other sex present and plants mostly dioecious; pollen trilobate; fruit with the viscous layer outside the vascular bundles; embryo suspensor long, multiseriate **Loranthaceae**

References: Barlow, B.A., *Austral. J. Bot.* 22 (1974) 531–621; in D.M. Calder & P. Bernhardt (eds.), *The Biology of Mistletoes* (1983) 19–46; *Blumea* 36 (1992) 293–381; *Blumea* 38 (1993) 65–126. — Barlow, B.A., F.G. Hawksworth, J. Kuijt, R.M. Polhill & D. Wiens, *The Golden Bough* 11 (1989) 1–4 (*Roy. Bot. Gard., Kew*). — Danser, B.H., *Bull. Jard. Bot. Buitenzorg III*, 11 (1931) 233–519; *Verh. Kon. Akad. Wet. Amsterdam, Afd. Natuurk., Sect. 2*, 29 (1933) 1–128; *Philipp. J. Sc.* 58 (1935) 1–128.

PLANT GEOGRAPHY

Because of the nature of the seed dispersal mechanism, dispersability in loranth is normally very low (Barlow & Schodde 1993). The family has a strongly continental distribution, with occurrences on remote islands being exceptional. It is probable that the present distribution of the family has been established primarily through migration over continuous land surfaces, and this allows high confidence in the correlation of phylogeny and migration.

The historical biogeography of the *Loranthaceae* is interpreted from the morphological, systematic and karyological data (for summary see Barlow 1990). The most primitive extant genera are all small, with relatively restricted areas, confined almost exclusively to Gondwanan land surfaces, and mostly in temperate habitats. They appear to be relictual endemics, and their scattered occurrence in the southern lands strongly suggests that the *Loranthaceae* are an old southern family. The loranth presumably originated in the mesic, warm to mild, closed forests of Gondwana, and the parasitic habit presumably did not arise in response to water stress but to competition for nutrients in complex ecosystems. Different phyletic stocks of *Loranthaceae* probably were dispersed with the separation of the Gondwanan fragments.

The Malesian loranth flora is clearly a composite one. Different lineages of *Loranthaceae* were well established on both sides of Charles's Line (Audley-Charles 1981) at the time of the Miocene contact between the Australian and Sunda plates. Phytogeographic patterns in the *Loranthaceae* with respect to Charles's Line range from localized species transgressions to differentiation and diversification of new genera from intrusive stocks which have crossed the Line, indicating prolonged exchange, perhaps continuously since migration first became possible after the Miocene contact. Because loranth are not directly dependent on soil or rainfall, and in Malesia are mostly of low host specificity, their habitat requirement is essentially a susceptible host tree. New habitats may have been readily available and two-way dispersal of loranth may have quickly followed the Miocene contact. *Cecarria* and *Amyema* have crossed from the east, and *Decaisnina*, *Cyne*, *Amylothea*, *Macrosolen*, *Lepeostegeres* and *Dendrophthoe* from the west, along with the progenitors of the Australian genus *Lysiana*.

At generic level, the Malesian loranth flora is also largely an immigrant one. Several genera of western Malesia, including *Macrosolen*, *Helixanthera*, *Dendrophthoe* and *Scurrula*, are widespread on the Asian mainland. They represent the ancestral stocks from which some endemic Malesian genera such as *Lepeostegeres*, *Lepidaria* and *Triethecanthera* have been derived. This component of the Malesian loranth flora is therefore Laurasian, probably established there following the original Gondwanan fragmentation (Barlow 1990). Similarly *Amyema* is widespread in Australia, and endemic genera such as *Dactylophora*, *Distrianthes*, *Sogerianthe* and *Papuanthes* are Papuan derivatives. The entire loranth flora of Malesia is therefore derived from two immigrant stocks, one Laurasian and the other Papuan, and both stocks have generated some small endemic genera and numerous endemic species.

References: Audley-Charles, M.G., in T.C. Whitmore (ed.), *Wallace's Line and Plate Tectonics* (1931) 24–35. — Barlow, B.A., in P. Baas et al. (eds.), *The Plant Diversity of Malesia* (1990) 273–292. — Barlow, B.A. & R. Schodde, *Beaufortia* 43 (1993) 124–129.

KEY TO THE GENERA

Owing to the general uniformity of growth habit, leaf morphology and fruit structure in Malesian *Loranthaceae*, it is not possible to generate keys based solely on vegetative and/or fruit characters. Diagnosis and identification of genera depends principally on inflorescence and floral characters, and is usually very difficult if they are not available. Inflorescence structures can sometimes be deduced from fruiting specimens if attention is given to the disposition of bracts and the scars of fallen parts.

- 1a. Inflorescence developing in a shallow depression, under a bubble-like calyptra of one piece formed from the stem periderm and falling or rupturing irregularly as the inflorescence develops beneath it **Cyne** (p. 284)
- b. Inflorescence externally visible from an early stage, not developing under a calyptra 2
- 2a. Inflorescence a head with an involucre of enlarged imbricate or valvate bracts completely or partially enclosing the flowers 3
- b. Inflorescence not a head, or if so, with floral bracts not enlarged and imbricate or valvate, nor forming an involucre around the entire inflorescence 10
- 3a. Involucral bracts 2, connate at the margins 4
- b. Involucral bracts 4 or more, free, usually imbricate 5
- 4a. Flowers in the inflorescence 6 in 2 opposite triads, sessile **Distrianthes** (p. 324)
- b. Flowers in the inflorescence 8–12 in 2 opposite rows, pedicellate and with a bract at the apex of each pedicel **Papuanthes** (p. 379)
- 5a. Flowers in the inflorescence (at least the outer ones) grouped in triads 6
- b. Flowers in the inflorescence not grouped in triads 9
- 6a. Petals free **Amyema** (p. 228)
- b. Petals fused to the middle or higher 7
- 7a. Inflorescence in reality a subumbellate raceme of triads tightly crowded at the apex of the axis, with narrow involucral segments developed from the bracts of the outer flowers and fused to the pedicels and rays **Lampas** (p. 339)
- b. Inflorescence distinctly capitate, the flowers inserted on a flat receptacle, with broad involucral segments developed from nonfertile bracts 8
- 8a. Inflorescence triads in the axils of enlarged bracts, with each flower surrounded by 3 smaller bracts **Thaumasianthes** (p. 394)
- b. Inflorescence triads not in the axils of enlarged bracts (except the outer triads), with each flower subtended by a single small bract **Lepeostegeres** (p. 340)
- 9a. Involucral bracts subtending the individual flowers **Elytranthe** (p. 326)
- b. Involucral bracts tightly enclosing the whole inflorescence ... **Lepidaria** (p. 348)

- 10a. Flowers in simple dichasia (triads or rarely tetrads), these in most species aggregated into larger racemose or umbellate inflorescences 11
 - b. Flowers single in the inflorescences (racemes, spikes, umbels, heads or solitary flowers) 17
- 11a. Petals fused to the middle or higher (sometimes with the corolla tube deeply split on one side) 12
 - b. Petals free completely or almost to the base (sometimes coherent for some time after anthesis) 15
- 12a. Anthers dorsifixed **Loxanthera** (p. 357)
 - b. Anthers basifixed 13
- 13a. Inflorescence a subumbellate raceme of triads tightly crowded at the apex of the axis, with narrow involuclal segments developed from the bracts of the outer flowers and fused to the pedicels and rays **Lampas** (p. 339)
 - b. Inflorescence umbellate or racemose but lacking an involucre of enlarged bracts 14
- 14a. Inflorescence umbellate **Amyema** (p. 228)
 - b. Inflorescence racemose **Amylothea** (p. 276)
- 15a. Inflorescence umbellate, sometimes contracted to a head **Amyema** (p. 228)
 - b. Inflorescence racemose 16
- 16a. Inflorescence a raceme with whorls of triads **Dactyliophora** (p. 289)
 - b. Inflorescence a raceme with decussate triads **Decaisnina** (p. 292)
- 17a. Petals fused to the middle or higher (sometimes with the corolla tube deeply slit on one side) 18
 - b. Petals free completely or almost to the base (sometimes coherent for some time after anthesis) 25
- 18a. Corolla 6-merous 19
 - b. Corolla 5- or 4-merous 23
- 19a. Bracts 3 under each flower, sometimes partly united 20
 - b. Bracts single under each flower 22
- 20a. Inflorescence a solitary flower on a short pedicel which is sometimes articulate ..
..... **Sogerianthe** (p. 388)
 - b. Inflorescence a spike or raceme 21
- 21a. Inflorescence axis decussately flattened, with the flowers borne in hollows
..... **Elytranthe** (p. 326)
 - b. Inflorescence axis terete or quadrangular, with the flowers not borne in hollows
..... **Macrosolen** (p. 358)
- 22a. Flowers strongly reflexed upwards from a vertical axis; corolla thick, more than 60 mm long **Trithecanthera** (p. 396)
 - b. Flowers not reflexed on the axis; corolla thin, less than 60 mm long
..... **Amylothea** (p. 276)
- 23a. Fruit obovoid, club-like, distinctly stipitate **Scurrula** (p. 381)
 - b. Fruit ovoid or ellipsoid, not stipitate 24

- 24a. Inflorescence racemose (sometimes few-flowered and subumbellate); corolla 5- or rarely 4-merous, regular or slightly zygomorphic; leaves mostly alternate **Dendrophthoe** (p. 307)
- b. Inflorescence a few-flowered umbel; corolla (in Malesia) 4-merous, zygomorphic; leaves opposite **Taxillus** (p. 392)
- 25a. Anthers dorsifixed, versatile **Cecarria** (p. 283)
- b. Anthers basifixed, immobile 26
- 26a. Inflorescence a simple umbel or solitary flower **Amyema** (p. 228)
- b. Inflorescence a raceme, spike or contracted to a head 27
- 27a. Inflorescence sessile, capitate, a very condensed spike without involucre **Barathranthus** (p. 279)
- b. Inflorescence a raceme or spike 28
- 28a. Flowers hermaphrodite; anthers linear **Helixanthera** (p. 328)
- b. Flowers mostly unisexual; anthers globose or subglobose . **Loranthus** (p. 354)

AMYEMA

Amyema Tiegh., Bull. Soc. Bot. France 41 (1894) 499. — Type species: *Amyema congener* (Sieber ex Schult. & Schult. f.) Tiegh., lecto.

Rhizomonanthes Danser, Verh. Kon. Ned. Akad. Wet. Amst. Afd. Natuurk., Sect. 2, 29 (1933) 100. — Type species: *Rhizomonanthes curvifolia* (K. Krause) Danser, *R. hastifolia* (Ridl.) Danser, *R. heterochroma* (K. Krause) Danser, syntypes.

[For extensive additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 318; Philipp. J. Sc. 58 (1935) 61; Barlow, Austral. J. Bot 14 (1966) 452; 22 (1974) 561].

Aerial stem-parasitic shrubs, with or without epicortical runners bearing secondary haustoria. *Leaves* opposite or verticillate, sometimes displaced and appearing alternate; venation pinnate or curvinerved. *Inflorescences* usually axillary, sometimes borne on internodes and/or epicortical runners, basically a pedunculate umbel of dichasia (triads or tetrads), but variously reduced in some species, to a head or simple umbel or solitary flower; rays of the umbel 1–50; bract usually single under each flower, simple or rarely lobed or with a dorsal protuberance. *Corolla* mostly 4- to 6-merous, mostly choripetalous but sometimes with petals coherent into a short tube. *Anthers* basifixed, immobile. *Style* simple, usually with a knob-like stigma. *Fruit* ellipsoid to ovoid or obovoid. — **Fig. 3–9.**

Distribution — Genus of 91 species distributed from the Southeast Asian mainland to Australia and islands of the southwestern Pacific as far as Samoa. In *Malesia* 59 species mostly in the east and south, with centres of diversity in the Philippines and New Guinea.

Habitat — Humid and open forests and disturbed sites, from lowlands to subalpine communities at 3750 m altitude. In some cases related species show altitudinal zonation, and many species accordingly have small areas in upland habitats. Among lowland species, some are widespread across several islands, whilst others are local endemics.

Ecology — Some species are aggressive, often occurring on cultivated trees. Host specificity varies between species, some having broad host ranges and others having a single preferred host genus or species. Most species of humid forests have low host specificity, occurring on a wide range of dicotyledonous hosts. This is the case even in mangrove communities, where the *Amyema* species usually occur on several host genera. In seasonal open forests and woodlands the *Amyema* species may be more closely adapted to parasitize the dominant tree species. In Australia many species show close visual resemblance to common hosts, and mimicry has been suggested.

Biogeography — The genus is a significant representative of the Australian/Papuan element in the Malesian flora. For discussion see Barlow, *Blumea* 36 (1992) 293.

Taxonomy — For a conspectus of the entire genus, and discussion of species circumscription, relationships and differences, see Barlow, *Blumea* 36 (1992) 293.

KEY TO THE SPECIES

Separate regional keys for Indonesia, the Philippines, New Guinea follow the main key.

- 1a. Leaves with opposite and decussate phyllotaxy, although sometimes displaced 2
- b. Leaves with verticillate phyllotaxy, usually ternate or quaternate, sometimes up to 8-verticillate, sometimes displaced to irregular spirals 49
- 2a. Inflorescence a pedunculate umbel of 2 or more triads or tetrads 3
- b. Inflorescence other than a pedunculate umbel of triads or tetrads (e.g., a head, simple umbel, solitary flower or sessile cluster) 32
- 3a. Flowers in triads 4
- b. Flowers in tetrads 31
- 4a. Triads with all flowers closely sessile 5
- b. Triads with at least the lateral flowers pedicellate, sometimes very shortly so . 13
- 5a. Rays in the umbel 2–4 6
- b. Rays in the umbel 5 or more 10
- 6a. Corolla 4-merous **4. *A. arthrocaulis***
- b. Corolla 5- or 6-merous 7
- 7a. Leaves sessile, cordate at the base **12. *A. cercidioides***
- b. Leaves petiolate (sometimes very shortly), attenuate or contracted at the base . 8
- 8a. Corolla in mature bud obtuse, 14–18 mm long; anther equal to the free part of the filament **53. *A. tristis***
- b. Corolla in mature bud acute, 20–40 mm long; anther much shorter than the free part of the filament 9
- 9a. Flowers in a linear row in the triad, the bracts not together forming a cupule subtending the triad **3. *A. artensis***
- b. Flowers in an equilateral disposition in the triad, the bracts together forming a subtending cupule **9. *A. caudiciflora***
- 10a. Rays in the umbel 10–30 **29. *A. incarnatiflora***
- b. Rays in the umbel 5–8 11

- 11a. Leaf lamina mostly acute and acuminate at the apex; anther longer than the free part of the filament **22. *A. friesiana***
- b. Leaf lamina obtuse or rounded at the apex; anther shorter than the free part of the filament 12
- 12a. Corolla in mature bud 18–20 mm long; anthers c. 1.5 mm long; leaf lamina often folded **52. *A. triantha***
- b. Corolla in mature bud 20–40 mm long; anthers 2–3 mm long; leaf lamina flat ..
..... **9. *A. caudiciflora***
- 13a. Leaves curvinerved; haustorial attachment single; epicortical runners lacking . 14
- b. Leaves pinninerved; haustorial attachments numerous, arising from epicortical runners 17
- 14a. Ovary white- or pale brown-tomentose in the lower part, glabrous above
..... **13. *A. conspicua***
- b. Ovary glabrous or with a uniformly sparse indumentum 15
- 15a. Corolla in the mature bud ridged or winged longitudinally . . **35. *A. miraculosa***
- b. Corolla in the mature bud terete or angular but not ridged or winged longitudinally 16
- 16a. Corolla 4-merous, with a globular inflation at the base in the mature bud; anthers transversely septate **23. *A. gravis***
- b. Corolla 5-merous, uniformly slender in the mature bud; anthers not transversely septate **34. *A. mackayensis***
- 17a. Rays in the umbel mostly 2 or 3 18
- b. Rays in the umbel mostly 4 or 5 19
- c. Rays in the umbel 6 or more 24
- 18a. Corolla 4-merous; leaf lamina mostly less than 1 cm wide . . . **31. *A. kebarensis***
- b. Corolla 5-merous; leaf lamina mostly more than 2 cm wide **3. *A. artensis***
- 19a. Corolla mostly 5-merous 20
- b. Corolla 4-merous 23
- 20a. Central flowers of the triads mostly pedicellate **11. *A. celebica***
- b. Central flowers of the triads sessile 21
- 21a. Inflorescence parts robust; bracts of the lateral flowers of the triads appressed to the ovary and enclosing it in early bud stages **41. *A. queenslandica***
- b. Inflorescence parts slender; bracts of the lateral flowers spreading 22
- 22a. Leaves dull on both sides; corolla 14–20 mm long; inflorescence and ovary glabrous **36. *A. novaebritanniae***
- b. Leaves usually more lustrous or glossy above; corolla 20–40 mm long; inflorescence and ovary usually shortly tomentose **3. *A. artensis***
- 23a. Floral bract with a complex dorsal protuberance; inflorescence peduncle very slender, more than 18 mm long **14. *A. corniculata***
- b. Floral bract constricted near the apex forming a simple dorsal protuberance; inflorescence peduncle slender to robust, less than 18 mm long . . . **37. *A. pachypus***
- 24a. Rays in the umbel 15 or more, arising from depressions in a globular dilation of the peduncle apex 25

- b. Rays in the umbel 6–12, not arising from depressions in a dilated peduncle apex or if so then the dilation not globular 26
- 25a. Leaf lamina broadly ovate to orbicular; indumentum red-brown; corolla c. 50 mm long, distinctly choripetalous **49. *A. stronglylophylla***
- b. Leaf lamina narrow lanceolate to ovate; indumentum tawny brown; corolla 30–40 mm long, petals often cohering at the base long after anthesis **24. *A. haenkeana***
N.B. See also *Dactyliophora verticillata*, in which reduced inflorescences can resemble those of *Amyema*.
- 26a. Corolla 4-merous 27
- b. Corolla 5- or 6-merous 28
- 27a. Peduncle 11–16 mm long, not strongly dilated at the apex . . **30. *A. irrubescens***
- b. Peduncle 20–45 mm long, dilated to c. 2 mm wide at the apex **59. *A. wichmannii***
- 28a. Corolla in mature bud 14–20 mm long **36. *A. novaebritanniae***
- b. Corolla in mature bud more than 25 mm long 29
- 29a. Leaf lamina lanceolate to oblong-ovate, up to 3 cm wide, acute at the apex; peduncle slender but dilated at the apex **55. *A. urdanetensis***
- b. Leaf lamina ovate to broadly spatulate or orbicular, more than 3 cm wide, rounded at the apex; peduncle uniformly robust 30
N.B. See also *Dactyliophora verticillata*, in which reduced inflorescences can resemble those of *Amyema*.
- 30a. Rays of the umbel 4–8; bracts of the lateral flowers of the triads c. 3 mm long, appressed to the ovary and enclosing it in early bud stages . **41. *A. queenslandica***
- b. Rays of the umbel 7–12; bracts of the lateral flowers up to 2 mm long, spreading **43. *A. rigidiflora***
- 31a. Tetrads with all flowers sessile; petals coherent at the base into a tube 4–5 mm long **50. *A. tetraflora***
- b. Tetrads with three flowers shortly pedicellate; petals coherent at the base into a tube 10–12 mm long **7. *A. brassii***
- 32a. Inflorescence a pedunculate or sessile 6- or 9-flowered head formed from 2 or 3 sessile triads 33
- b. Inflorescence not as above (a pedunculate or sessile simple umbel, a solitary flower or a 3-flowered head) 43
- 33a. Leaves sessile 34
- b. Leaves obscurely or distinctly petiolate 35
- 34a. Leaves truncate to cordate at the base; peduncle rudimentary (inflorescence sessile) **15. *A. cuernosensis***
- b. Leaves cuneate to truncate at the base; peduncle 2–5.5 mm long . **18. *A. edanoi***
- 35a. Corolla 4-merous; bracts c. 6 mm long **51. *A. tetrapetala***
- b. Corolla 5- or 6-merous; bracts less than 3 mm long 36
- 36a. Petals with deflexed spurs on the inside above the base forming a nectar chamber 37
- b. Petals lacking deflexed spurs on the inside above the base 39

- 37a. Inflorescence peduncle 5–11 mm long; leaf lamina obtuse or rounded at the apex **32. *A. longipes***
- b. Inflorescence peduncle mostly 2–4 mm long 38
- 38a. Leaf lamina acuminate at the apex, mostly more than 12 cm long; bracts of the lateral flowers appressed to the ovary **47. *A. seriata***
- b. Leaf lamina acute at the apex, mostly less than 12 cm long; bracts of the lateral flowers spreading **53. *A. tristis***
- 39a. Leaves glossy grey/green above and dull brown below 40
- b. Leaves dull on both sides at least when dry 41
- 40a. Inflorescence peduncle up to 3 mm long; anther about equal to the free part of the filament **27. *A. hexameris***
- b. Inflorescence peduncle 5–9 mm long; anther much shorter than the free part of the filament **3. *A. artensis***
- 41a. Inflorescence sessile; petiole broad, 1–3 mm long **2. *A. apoensis***
- b. Inflorescence pedunculate; petiole slender 42
- 42a. Inflorescence peduncle 4–5 mm long; petiole distinct, 5–15 mm long **28. *A. hexantha***
- b. Inflorescence peduncle usually 2–4 mm long; petiole obscure, 0.5–4 mm long **53. *A. tristis***
- 43a. Inflorescence a pedunculate capitulum formed from a single cymule of 3 sessile flowers; **10. *A. cauliflora***
- b. Inflorescence a simple umbel 44
- c. Inflorescence a single flower, usually on an articulate pedicel 47
- 44a. Peduncle of the umbel obsolete or up to 1 mm long 45
- b. Peduncle of the umbel distinct, usually more than 2 mm long 46
- 45a. Corolla 8–22 mm long; leaf rounded or obtuse at the apex **5. *A. beccarii***
- b. Corolla 25–40 mm long; leaf acuminate and acute at the apex **48. *A. squarrosa***
- 46a. Rays of the umbel 2 **46. *A. seemeniana***
- b. Rays of the umbel c. 12 **54. *A. umbellata***
- 47a. Corolla 5- or 6-merous, 8–22 mm long **5. *A. beccarii***
- b. Corolla 4-merous, mostly 20–45 mm long 48
- 48a. Leaves 4–7 cm long, acuminate acute, almost sessile; articulate peduncle c. 3 mm long **26. *A. hastifolia***
- b. Leaves 1.8–4 cm long, rounded, distinctly petiolate; articulate peduncle 4–8 mm long **21. *A. finisterrae***
- 49a. Inflorescence a pedunculate umbel of 2 or more triads or tetrads 50
- b. Inflorescence other than a pedunculate umbel of triads or tetrads (e.g., a head, simple umbel, solitary flower or sessile cluster) 68
- 50a. Flowers in tetrads **17. *A. dilatipes***
- b. Flowers in triads 51
- 51a. Triads with all flowers sessile 52
- b. Triads with at least the lateral flowers pedicellate 56

- 52a. Rays in the umbel more than 10 **29. *A. incarnatiflora***
- b. Rays in the umbel 4–8 53
- c. Rays in the umbel 2–3 55
- 53a. Leaves mostly in regular whorls of 5 or 6, rarely quaternate ... **44. *A. scandens***
- b. Leaves ternate or rarely quaternate, frequently scattered 54
- 54a. Leaves sessile or sometimes minutely petiolate **9. *A. caudiciflora***
- b. Leaves petiolate **38. *A. plicatula***
- 55a. Leaf lamina linear-lanceolate, concave above, less than 1 cm wide **8. *A. canaliculata***
- b. Leaf lamina ovate or lanceolate-ovate, flat, more than 2 cm wide **56. *A. vernicosa***
- 56a. Rays in the umbel 2–5 57
- b. Rays in the umbel 6–14 63
- c. Rays in the umbel 15 or more 67
- 57a. Leaves sessile 58
- b. Leaves petiolate 60
- 58a. Leaves 7.5–10 cm long **42. *A. rhytidoderma***
- b. Leaves mostly less than 5 cm long 59
- 59a. Corolla more than 25 mm long, sparsely to densely hairy ... **33. *A. luzonensis***
- b. Corolla less than 21 mm long, glabrous **6. *A. benguetensis***
- 60a. Petals with dorsal appendages forming a crown near the apex of the flower bud **57. *A. verticillata***
- b. Petals without dorsal appendages 61
- 61a. Triads with the central flower sessile **3. *A. artensis***
- b. Triads with all flowers pedicellate 62
- 62a. Leaves regularly verticillate (mostly quaternate); lamina thin, mostly less than 8 cm long; petals usually 4 **1. *A. acuta***
- b. Leaves opposite, scattered or quaternate; lamina thickly coriaceous, mostly more than 8 cm long; petals usually 5 **11. *A. celebica***
- 63a. Rays of the umbel 6–8 64
- b. Rays of the umbel 9 or more 66
- 64a. Inflorescence axis more than 10 mm long; leaf lamina less than 10 cm long **1. *A. acuta***
- b. Inflorescence axis less than 10 mm long; leaf lamina more than 10 cm long ... 65
- 65a. Petals 5, coherent at the base for 1–3 mm **25. *A. halconensis***
- b. Petals 4, eventually free completely to the base **45. *A. scheffleroides***
- 66a. Leaves opposite, ternate or scattered ternate; lamina up to 10 cm long **30. *A. irrubescens***
- b. Leaves in whorls of 3–6; lamina 10–30 cm long **40. *A. polytrias***
- 67a. Inflorescence peduncle up to 10 mm long; petals 4 **16. *A. curranii***
- b. Inflorescence peduncle more than 25 mm long; petals 5 or 6 . **24. *A. haenkeana***
- 68a. Inflorescence a pedunculate or sessile 9-flowered head formed from 3 sessile triads 69

- b. Inflorescence not as above (a pedunculate or sessile simple umbel or a solitary flower) 70
- 69a. Leaf lamina less than 8 cm long; inflorescence peduncle 12–15 mm long; petals lacking a deflexed spur on the inside above the base **56. *A. vernicosa***
- b. Leaf lamina more than 8 cm long; inflorescence peduncle c. 1 mm long; petals with a deflexed spur on the inside above the base **19. *A. enneantha***
- 70a. Inflorescence a sessile 1- to 3-flowered umbel (i.e., the flowers sometimes seemingly solitary) 71
- b. Inflorescence a pedunculate simple umbel 72
- 71a. Leaf lamina narrowly to broadly obovate, mostly rounded at the apex, mostly less than 10 cm long; pedicels of the flowers distinct, mostly 1–4 mm long; anthers on a short free filament **5. *A. beccarii***
- b. Leaf lamina ovate, shortly acuminate and obtuse at the apex, mostly more than 12 cm long; pedicels of the flowers very short or absent so that the inflorescence resembles a sessile cluster; anthers sessile **58. *A. wenzelii***
- 72a. Rays of the umbel c. 12 **54. *A. umbellata***
- b. Rays of the umbel 3–6 73
- 73a. Peduncle of the umbel 2–5 mm long; corolla mostly less than 20 mm long **20. *A. fasciculata***
- b. Peduncle of the umbel 8–11 mm long; corolla more than 20 mm long **39. *A. polillensis***

KEY TO THE SPECIES OF INDONESIA (EXCL. IRIAN JAYA) AND MALAYSIA

- 1a. Inflorescence a pedunculate umbel of 2 or more triads 2
- b. Inflorescence other than a pedunculate umbel of triads (e.g., a head, simple umbel, solitary flower or sessile cluster) 10
- 2a. Triads with all flowers closely sessile 3
- b. Triads with at least the lateral flowers pedicellate, sometimes very shortly so .. 4
- 3a. Rays in the umbel 2–4; corolla 14–18 mm long; anther equal to the free part of the filament; leaf lamina flat **53. *A. tristis***
- b. Rays in the umbel 5 or more; corolla 18–20 mm long; anther much shorter than the free part of the filament; leaf lamina often folded **52. *A. triantha***
- 4a. Rays in the umbel 2–5 5
- b. Rays in the umbel 6 or more 7
- 5a. Rays in the umbel mostly 4 or 5; central flowers of the triads mostly pedicellate .. **11. *A. celebica***
- b. Rays in the umbel mostly 2 or 3; central flowers of the triads sessile 6
- 6a. Corolla in mature bud ridged or winged longitudinally, lacking a globular inflation at the base; anthers not transversely septate **35. *A. miraculosa***
- b. Corolla in mature bud terete or angular but not ridged or winged longitudinally, with a globular inflation at the base; anthers transversely septate ... **23. *A. gravis***

- 7a. Corolla 5- or 6-merous; triads with the central flower sessile; leaves opposite ... **43. *A. rigidiflora***
- b. Corolla 4-merous; triads with all flowers shortly pedicellate; leaves rarely opposite, mostly in whorls of 3–6 (rarely scattered) 8
- 8a. Rays of the umbel 6–8; peduncle less than 10 mm long .. **45. *A. scheffleroides***
- b. Rays of the umbel 9 or more; peduncle more than 10 mm long 9
- 9a. Leaves opposite, ternate or scattered ternate; lamina up to 10 cm long **30. *A. irrubescens***
- b. Leaves in whorls of 3–6; lamina 10–30 cm long **40. *A. polytrias***
- 10a. Inflorescence a pedunculate or sessile 6- or 9-flowered head formed from 2 or 3 sessile triads 11
- b. Inflorescence not as above (a pedunculate or sessile simple umbel or a solitary flower) 16
- 11a. Leaves ternate; inflorescence 9-flowered **19. *A. enneantha***
- b. Leaves opposite; inflorescence 6-flowered 12
- 12a. Leaves sessile 13
- b. Leaves obscurely or distinctly petiolate 14
- 13a. Leaves truncate to cordate at the base; peduncle rudimentary (inflorescence sessile) **15. *A. cuernosensis***
- b. Leaves cuneate to truncate at the base; peduncle 2–5.5 mm long . **18. *A. edanoi***
- 14a. Leaves glossy grey/green above and dull brown below; petiole distinct, 5–10 mm long; inflorescence peduncle 0.5–2.5 mm long **27. *A. hexameres***
- b. Leaves dull on both sides at least when dry; petiole short or obscure, mostly less than 5 mm long; inflorescence peduncle usually 2–11 mm long 15
- 15a. Peduncle 5–11 mm long; leaf lamina obtuse or rounded at the apex **32. *A. longipes***
- b. Peduncle usually 2–4 mm long; leaf lamina acute at the apex **53. *A. tristis***
- 16a. Inflorescence a sessile 1- to 3-flowered umbel (i.e., the flowers sometimes seemingly solitary) **5. *A. beccarii***
- b. Inflorescence a pedunculate simple umbel 17
- 17a. Rays of the umbel c. 12; corolla 5- or 6-merous **54. *A. umbellata***
- b. Rays of the umbel 3–6; corolla mostly 4-merous **20. *A. fasciculata***

KEY TO THE PHILIPPINE SPECIES

- 1a. Inflorescence a pedunculate umbel of 2 or more triads 2
- b. Inflorescence other than a pedunculate umbel of triads (e.g., a head, simple umbel, solitary flower or sessile cluster) 13
- 2a. Triads with all flowers closely sessile 3
- b. Triads with at least the lateral flowers pedicellate 4
- 3a. Rays in the umbel more than 10, arising from depressions in a globular dilation of the end of the peduncle **29. *A. incarnatiflora***

- b. Rays in the umbel 3, arising at the end of an unthickened peduncle **56. *A. vernicosa***
- 4a. Rays in the umbel 2–5 5
 - b. Rays in the umbel 6–14 10
 - c. Rays in the umbel 15 or more 12
- 5a. Leaves sessile 6
 - b. Leaves petiolate 8
- 6a. Leaves 7.5–10 cm long **42. *A. rhytidoderma***
 - b. Leaves mostly less than 5 cm long 7
- 7a. Corolla more than 25 mm long, sparsely to densely hairy ... **33. *A. luzonensis***
 - b. Corolla less than 21 mm long, glabrous **6. *A. benguetensis***
- 8a. Petals with dorsal appendages forming a crown near the apex of the flower bud .. **57. *A. verticillata***
 - b. Petals without dorsal appendages 9
- 9a. Leaves regularly verticillate (mostly quaternate); lamina thin, mostly less than 8 cm long; petals usually 4 **1. *A. acuta***
 - b. Leaves opposite, scattered or quaternate; lamina thickly coriaceous, mostly more than 8 cm long; petals usually 5 **11. *A. celebica***
- 10a. Leaves opposite **55. *A. urdanetensis***
 - b. Leaves with verticillate phyllotaxy, sometimes displaced to irregular spirals .. 11
- 11a. Inflorescence axis more than 10 mm long; leaf lamina less than 10 cm long; petals 4, free to the base **1. *A. acuta***
 - b. Inflorescence axis less than 10 mm long; leaf lamina more than 10 cm long; petals 5, coherent at the base for 1–3 mm **25. *A. halconensis***
- 12a. Inflorescence peduncle up to 10 mm long; petals 4 **16. *A. curranii***
 - b. Inflorescence peduncle more than 25 mm long; petals 5 or 6 . **24. *A. haenkeana***
- 13a. Leaves with opposite and decussate phyllotaxy, although sometimes displaced 14
 - b. Leaves with verticillate phyllotaxy, usually ternate or quaternate, sometimes up to 8-verticillate, sometimes displaced to irregular spirals 21
- 14a. Inflorescence a pedunculate or sessile 6-flowered head formed from 2 sessile triads 15
 - b. Inflorescence not as above (a pedunculate or sessile simple umbel, a solitary flower or 3-flowered head)..... 19
- 15a. Leaves sessile 16
 - b. Leaves obscurely or distinctly petiolate 17
- 16a. Leaves truncate to cordate at the base; peduncle rudimentary (inflorescence sessile) **15. *A. cuernosensis***
 - b. Leaves cuneate to truncate at the base; peduncle 2–5.5 mm long . **18. *A. edanoi***
- 17a. Petals with deflexed spurs on the inside above the base forming a nectar chamber; bracts of the lateral flowers appressed to the ovary, not forming part of the involucre **47. *A. seriata***
 - b. Petals lacking deflexed spurs on the inside above the base; bracts of the lateral flowers spreading, forming part of the involucre 18

- 18a. Inflorescence sessile; petiole broad, 1–3 mm long **2. *A. apoensis***
 b. Inflorescence peduncle 4–5 mm long; petiole slender, 5–15 mm long **28. *A. hexantha***
- 19a. Inflorescence a pedunculate capitulum formed from a single cymule of 3 sessile flowers **10. *A. cauliflora***
 b. Inflorescence a simple umbel or solitary flower 20
- 20a. Inflorescence a sessile 1- to 3-flowered umbel (i.e., the flowers sometimes seemingly solitary); pedicels of the flowers mostly 1–4 mm long; corolla 5- or 6-merous **5. *A. beccarii***
 b. Inflorescence a pedunculate 2- to 4-flowered simple umbel; the peduncle 2–5 mm long; pedicels mostly 2–3 mm long; corolla mostly 4-merous **20. *A. fasciculata***
- 21a. Inflorescence a 9-flowered head formed from 3 sessile triads, on a peduncle 12–15 mm long **56. *A. vernicosa***
 b. Inflorescence not as above (a pedunculate or sessile simple umbel or a solitary flower) 22
- 22a. Inflorescence a sessile 1- to 3-flowered umbel (i.e., the flowers sometimes seemingly solitary) 23
 b. Inflorescence a pedunculate simple umbel 24
- 23a. Leaf lamina narrowly to broadly obovate, mostly rounded at the apex, mostly less than 10 cm long; pedicels of the flowers distinct, mostly 1–4 mm long; anthers on a short free filament **5. *A. beccarii***
 b. Leaf lamina ovate, shortly acuminate and obtuse at the apex, mostly more than 12 cm long; pedicels of the flowers very short or absent so that the inflorescence resembles a sessile cluster; anthers sessile **58. *A. wenzelii***
- 24a. Umbel 2- to 4-flowered; peduncle 2–5 mm long; corolla mostly less than 20 mm long; leaves 2- to 4-verticillate **20. *A. fasciculata***
 b. Umbel 4- to 6-flowered; peduncle 8–11 mm long; corolla more than 20 mm long; leaves 4- to 7-verticillate **39. *A. polillensis***

KEY TO THE NEW GUINEAN SPECIES (INCL. BISMARCK ARCH.)

- 1a. Leaves with opposite and decussate phyllotaxy, although sometimes displaced 2
 b. Leaves with verticillate phyllotaxy, usually ternate or quaternate, sometimes up to 8-verticillate, sometimes displaced to irregular spirals 28
- 2a. Inflorescence a pedunculate umbel of 2 or more triads or tetrads 3
 b. Inflorescence other than a pedunculate umbel of triads or tetrads (e.g., a head, simple umbel, solitary flower or sessile cluster) 23
- 3a. Flowers in triads 4
 b. Flowers in tetrads 22
- 4a. Triads with all flowers closely sessile 5
 b. Triads with at least the lateral flowers pedicellate, sometimes very shortly 9

- 5a. Corolla 4-merous **4. A. arthrocaulis**
 b. Corolla 5- or 6-merous 6
- 6a. Leaves sessile or with a short obscure petiole rarely 3 mm long 7
 b. Leaves with distinct petioles mostly more than 4 mm long 8
- 7a. Leaves almost orbicular, cordate at the base **12. A. cercidioides**
 b. Leaves mostly ovate or obovate (rarely narrower), attenuate or cuneate at the base **9. A. caudiciflora**
- 8a. Flowers in a linear row in the triad, the bracts not together forming a cupule subtending the triad; rays in the umbel 2–4 **3. A. artensis**
 b. Flowers in an equilateral disposition in the triad, the bracts together forming a subtending cupule; rays in the umbel 5–8 **22. A. friesiana**
- 9a. Rays in the umbel 2–5 10
 b. Rays in the umbel 6 or more 18
- 10a. Leaves curvinerved; haustorial attachments lacking epicortical runners 11
 b. Leaves pinninerved; haustorial attachments on epicortical runners 12
- 11a. Inflorescence axis and rays tomentose; ovary white- or pale brown-tomentose in the lower part, glabrous above **13. A. conspicua**
 b. Inflorescence axis and rays glabrous; ovary glabrous or with a uniformly sparse indumentum **34. A. mackayensis**
- 12a. Corolla 4-merous 13
 b. Corolla mostly 5-merous 16
- 13a. Leaf lamina mostly less than 1 cm wide **31. A. kebarensis**
 b. Leaf lamina mostly more than 2 cm wide 14
- 14a. Leaf lamina 10–15 cm long; corolla 35–40 mm long **3. A. artensis**
 b. Leaf lamina less than 8 cm long; corolla 15–20 mm long 15
- 15a. Floral bract with a complex dorsal protuberance; inflorescence peduncle very slender, more than 18 mm long **14. A. corniculata**
 b. Floral bract constricted near the apex forming a simple dorsal protuberance; inflorescence peduncle slender to robust, less than 18 mm long **37. A. pachypus**
- 16a. Inflorescence parts robust; bracts of the lateral flowers of the triads appressed to the ovary and enclosing it in early bud stages **41. A. queenslandica**
 b. Inflorescence parts slender; bracts of the lateral flowers spreading 17
- 17a. Leaves dull on both sides; corolla 14–20 mm long; inflorescence and ovary glabrous **36. A. novaebritanniae**
 b. Leaves usually more lustrous or glossy above; corolla 20–40 mm long; inflorescence and ovary usually shortly tomentose **3. A. artensis**
- 18a. Rays in the umbel 15 or more, arising from depressions in a globular dilation of the peduncle apex **49. A. strongylophylla**
 N.B. See also *Dactylophora verticillata*, in which reduced inflorescences can resemble those of *Amyema*.
 b. Rays in the umbel 6–12, not arising from depressions in a dilated peduncle apex or if so then the dilation not globular 19

- 19a. Corolla 4-merous; inflorescence peduncle distinctly widened upwards **59. *A. wichmannii***
 b. Corolla 5- or 6-merous; inflorescence peduncle not widened upwards 20
- 20a. Corolla in mature bud 14–20 mm long **36. *A. novaebritanniae***
 b. Corolla in mature bud more than 25 mm long 21
- 21a. Rays of the umbel 4–8; bracts of the lateral flowers of the triads c. 3 mm long, appressed to the ovary and enclosing it in early bud stages . **41. *A. queenslandica***
 b. Rays of the umbel 7–12; bracts of the lateral flowers up to 2 mm long, spreading **43. *A. rigidiflora***
 N.B. See also *Dactyliophora verticillata*, in which reduced inflorescences can resemble those of *Amyema*.
- 22a. Tetrads with all flowers sessile; petals coherent at the base into a tube 4–5 mm long **50. *A. tetraflora***
 b. Tetrads with three flowers shortly pedicellate; petals coherent at the base into a tube 10–12 mm long **7. *A. brassii***
- 23a. Inflorescence a pedunculate or sessile 6-flowered head formed from two sessile triads 24
 b. Inflorescence not as above (a pedunculate or sessile simple umbel, a solitary flower or a head of 3–5 flowers) 25
- 24a. Corolla 4-merous; central bracts of the triads c. 6 mm long **51. *A. tetrapetala***
 b. Corolla 5- or 6-merous; central bracts of the triads less than 3 mm long **3. *A. artensis***
- 25a. Inflorescence a simple umbel 26
 b. Inflorescence a single flower, usually on an articulate pedicel 27
- 26a. Peduncle of the umbel obsolete or up to 1 mm long; leaf lamina weakly pinninerved, the main lateral veins diverging from near the base ... **48. *A. squarrosa***
 b. Peduncle of the umbel distinct, usually more than 2 mm long; leaf lamina distinctly curvinerved from the base **46. *A. seemeniana***
- 27a. Leaves 4–7 cm long, acuminate acute, almost sessile; articulate peduncle c. 3 mm long **26. *A. hastifolia***
 b. Leaves 1.8–4 cm long, rounded, distinctly petiolate; articulate peduncle 4–8 mm long **21. *A. finisterrae***
- 28a. Inflorescence a 2- to 4-flowered simple umbel **20. *A. fasciculata***
 b. Inflorescence a pedunculate umbel of 2 or more triads or tetrads 29
- 29a. Flowers in tetrads **17. *A. dilatipes***
 b. Flowers in triads 30
- 30a. Triads with at least the lateral flowers pedicellate **3. *A. artensis***
 b. Triads with all flowers sessile 31
- 31a. Rays in the umbel 2 or 3; leaf lamina linear-lanceolate, concave above, less than 1 cm wide **8. *A. canaliculata***
 b. Rays in the umbel 4–8; leaf lamina lanceolate to nearly orbicular, flat, more than 1 cm wide 32

- 32a. Leaves mostly in regular whorls of 5 or 6, rarely quaternate . . . **44. *A. scandens***
 b. Leaves ternate or rarely quaternate, frequently scattered 33
 33a. Leaves sessile or sometimes with a very short thick petiole . . . **9. *A. caudiciflora***
 b. Leaves distinctly petiolate **38. *A. plicatula***

1. *Amyema acuta* (Tiegh.) Danser

Amyema acuta (Tiegh.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 293. — *Stemmatophyllum acutum* Tiegh., Bull. Soc. Bot. France 41 (1894) 546. — Type: *Cuming* 1973, Philippines, Manila. [For synonymy see Danser, Philipp. J. Sc. 58 (1935) 74–78; Barlow, Blumea 36 (1992) 307].

Glabrous except for the young inflorescence and flowers sometimes softly pubescent. *Leaves* regularly verticillate (mostly quaternate); lamina lanceolate to ovate-lanceolate, mostly 5–10 cm long, mostly 1.5–4 cm wide, attenuate to shortly cuneate at the base to a petiole 3–10 mm long, mostly acuminate and acute at the apex, dull or slightly glossy above, dull and distinctly paler below; venation pinnate with the midrib prominent below. *Inflorescences* at the nodes, pedunculate, mostly 4- (rarely 2- to 6-)rayed umbels of triads with all flowers pedicellate; peduncle 10–40(–60) mm long; rays 3–8 mm long; pedicels 1–2 mm long. *Corolla* in mature bud mostly 4-merous, 18–28 mm long, slender, weakly clavate and obtuse at the apex, frequently red below and orange or yellow above. *Anther* 2–3 mm long, about equal to the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — Recorded from primary forests, mostly from 1200 to 2400 m altitude, rarely down to 600 m; no hosts recorded.

Note — Closely related to *Amyema celebica*; for differences see Barlow, Blumea 36 (1992) 307, 320.

2. *Amyema apoensis* (Elmer) Barlow

Amyema apoensis (Elmer) Barlow, Blumea 36 (1992) 308. — *Loranthus apoensis* Elmer, Leaflet Philipp. Bot. 3 (1911) 1073. — *Dicymanthes apoensis* (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 311. — Type: *Elmer* 11454, lecto, Mindanao, Mt Apo.

Glabrous. *Leaves* opposite; lamina elliptic to broadly elliptic, 9–15 by 4–8 cm, shortly attenuate at the base to an obscure petiole 1–3 mm long, shortly acuminate and acute at the apex, dull on both sides when dry but slightly darker above; venation pinnate, faintly visible on both sides. *Inflorescences* at the nodes, a subsessile 6-flowered head of 2 sessile triads on a peduncle c. 0.5 mm long which is immersed in the bark. *Corolla* in mature bud 5-merous, 18–22 mm long, uniformly slender, mostly pink or red below and yellowish above. *Anther* 1.5–2 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: Philippines (Mindanao).

Habitat & Ecology — Humid forests, 1830–2130 m altitude; the only recorded host is *Ficus*.

Notes — 1. Closely related to *Amyema hexantha*, which is sympatric but occurs at lower altitudes; for distinction see Barlow, Blumea 36 (1992) 309.

2. For discussion of equivalence of *Dicymanthes* and *Amyema*, see Barlow, *Blumea* 36 (1992) 298.

3. *Amyema artensis* (Montrouz.) Danser

Amyema artensis (Montrouz.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 293; Barlow in Handb. Fl. Papua New Guinea 2 (1981) 209. — *Loranthus artensis* Montrouz., Mém. Acad. Lyon 10 (1860) 213. — Type: *Montrouzier 199*, New Caledonia, Ile Art.

Amyema wichmannii subsp. *aggregata* Barlow, Austral. J. Bot. 22 (1974) 598; in Handb. Fl. Papua New Guinea 2 (1981) 226; Van Royen, Alpine Fl. New Guinea 3 (1982) 2270. — Type: *Galore & Wood NGF 41009*, Papua New Guinea, Mt Simpson.

[For extensive additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 323, 344; 14 (1936) 88, 89; Barlow, Austral. J. Bot. 22 (1974) 564, 566; *Blumea* 36 (1992) 309].

Glabrous except for the inflorescence and ovary usually shortly and densely brown tomentose. *Leaves* opposite or in whorls of 3 or 4; lamina usually oblong to ovate or ob-ovate, rarely lanceolate, 4–9(–14) by 1.5–4(–7) cm, shortly cuneate to almost truncate at the base to a petiole (3–)5–8 mm long, obtuse or rounded (rarely acute or acuminate) at the apex, usually shining and often red above, dull below, often recurved at the margins; venation pinnate with the midrib and the main laterals visible on both sides. *Inflorescences* at the nodes, pedunculate 2- (rarely 3- to 5-)rayed umbels of triads with the central flowers sessile; peduncle (5–)8–20 mm long; rays 3–6 mm long; lateral flowers usually on pedicels 1–3 mm long but sometimes sessile. *Corolla* in mature bud 5-merous, 20–30 mm long, slender, weakly clavate and acute at the apex, mostly red or bright pink below and orange, yellow or paler pink above. *Anther* c. 1.5 mm long, about one fifth as long as the free part of the filament. — **Fig. 3a–c.**

Distribution — Western Pacific from Caroline Islands southeastwards to New Caledonia and Samoa; *Malesia*: New Guinea including Louisiade Archipelago.

Habitat & Ecology — Primary and secondary forests, in mainland New Guinea mostly from 1500 to 2500 m altitude, but recorded from 1190–3400 m; in other island groups from sea level to the highest altitudes which exist; recorded hosts too numerous to list.

Notes — 1. For discussion of species circumscription and relationships with *Amyema novaebritanniae* and *A. pachypus*, see Barlow, *Blumea* 36 (1992) 310.

2. For discussion of occurrence on remote Pacific islands, see Barlow & Schodde, *Beaufortia* 43 (1993) 124.

4. *Amyema arthrocaulis* Barlow

Amyema arthrocaulis Barlow, *Blumea* 36 (1992) 312. — Type: *Brass 11299*, Irian Jaya, Lake Habbema.

Glabrous. *Leaves* opposite; lamina oblanceolate to narrowly spatulate, 5–7 by 1–2 cm, gradually attenuate at the base to an obscure petiole 5–10 mm long, rounded at the apex, dull on both sides; venation pinnate with the midrib and the main laterals raised below but indistinct. *Inflorescences* at the nodes, pedunculate 4-rayed umbels of triads with all flowers sessile; peduncle 13–15 mm long; rays 5–8 mm long. *Corolla* in mature bud 4-merous, 26–30 mm long, uniformly slender, quadrangular when dry, acute at the

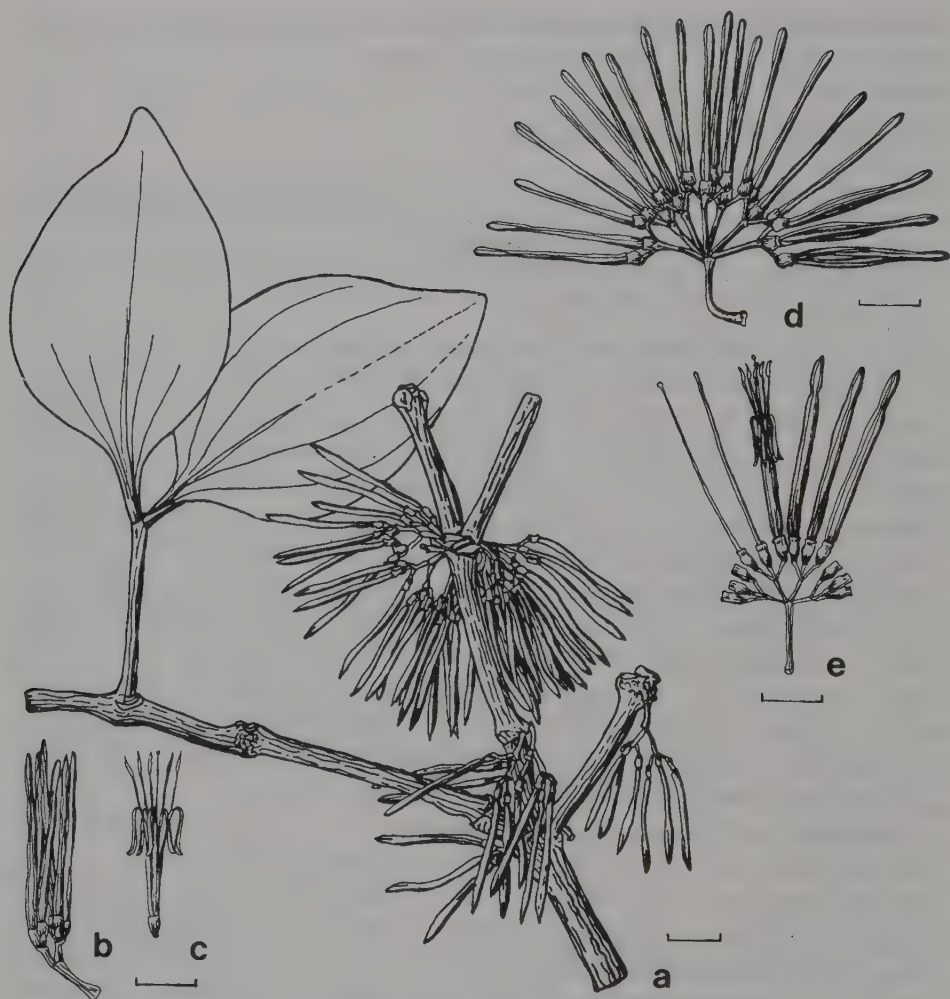


Fig. 3. *Amyema artensis* (Montrouz.) Danser. a. Twig with flower buds; b. inflorescence; c. flower. — *A. rigidiflora* (K. Krause) Danser. d. Inflorescence. — *A. celebica* (Tiegh.) Danser. e. Inflorescence (a: Ledermann 13363; b, c: Docters van Leeuwen 10989; d: Lam 2908; e: Lam 2648). Redrawn from Danser (1931). Scale bars represent 1 cm.

apex, red below and yellow above. *Anther* c. 2.5 mm long, with a short knob-like sterile tip, about half as long as the free part of the filament.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Known from type locality only, 2200 m altitude; no host recorded.

Note — Probably related to *Amyema scandens*; for distinction as a species see Barlow, *Blumea* 36 (1992) 312.

5. *Amyema beccarii* (Tiegh.) Danser

Amyema beccarii (Tiegh.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 294. — *Stemmatophyllum beccarii* Tiegh., Bull. Soc. Bot. France 41 (1894) 506, 546. — Type: *Beccari* 688, Sarawak.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 326; Philipp. J. Sc. 58 (1935) 87; Barlow, *Blumea* 36 (1992) 313].

Glabrous. *Leaves* usually quaternate, rarely decussate; lamina narrowly obovate to elliptic, mostly 4–10 cm long, mostly 2–5 cm wide, attenuate at the base to a petiole mostly 4–12 mm long, rounded to obtuse at the apex, dull on both sides; venation pinnate with the midrib raised in the basal part and otherwise obscure. *Inflorescences* many at the nodes and along the internodes and epicortical runners, sessile 1- to 3- (usually 2-) flowered umbels; pedicels (0.5–)2–4 mm long. *Corolla* in mature bud 5- or 6-merous, 13–22 mm long, usually slightly inflated at the base, rounded at the apex, mostly red, orange or yellow below and green above, sometimes with a purple zone at the tip. *Anther* 2–5 mm long, sessile or much longer than the free part of the filament. — **Fig. 4, 9g, h.**

Distribution — Thailand; *Malesia*: northern parts from Philippines to Bangka, Borneo, Celebes, Moluccas (Sulu Is, Taliabu).

Habitat & Ecology — Mostly in humid forests, 0–1300 m altitude; recorded hosts include *Barringtonia*, *Gonystylus*, *Melastoma*, *Palaquium*, *Psychotria*, and *Schima*.

Note — Closely related to *Amyema wenzelii*; the species can also be confused with *A. fasciculata*; for discussion see Barlow, *Blumea* 36 (1992) 314.



Fig. 4. *Amyema beccarii* (Tiegh.) Danser, node with several inflorescences. Borneo, W Kalimantan, Pasir Pandjang (*Elsener* H 93). Photo A. Elsener, 1965.

6. *Amyema benguetensis* (Merr.) Danser

Amyema benguetensis (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 294. — *Loranthus benguetensis* Merr., Philipp. J. Sc., Bot. 4 (1909) 134. — Type: Curran, Merritt & Zschokke FB 16064, lecto, Luzon, Mt Pulog.

Glabrous. *Leaves* quaternate, sessile, crowded on branchlets with short internodes; lamina narrowly oblong to ovate, mostly 2.5–5 cm long, 1–2 cm wide, cuneate at the base, shortly rounded to acute at the apex, glossy on both sides but darker above; venation pinnate with the midrib prominent below. *Inflorescences* at the nodes, pedunculate, (2–)4(–6)-rayed umbels of triads with all flowers pedicellate; peduncle 8–16 mm long; rays 2–4 mm long; pedicels 0.5–2 mm long. *Corolla* in mature bud 4- or 5-merous, 15–20 mm long, slender, weakly clavate and acute, yellow below and red above. *Anther* 2–2.5 mm long, narrowed upwards, with a broad connective, nearly twice as long as the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — Uplands from 1200 to 1600 m altitude; the only recorded host is *Pinus*. Hosts other than dicotyledons are rare in *Loranthaceae*.

Note — Closely related to *Amyema luzonensis* and *A. rhytidoderma*; for differences and species circumscription see Barlow, Blumea 36 (1992) 314.

7. *Amyema brassii* Barlow

Amyema brassii Barlow, Austral. J. Bot. 22 (1974) 568; in Handb. Fl. Papua New Guinea 2 (1981) 210; Blumea 36 (1992) 317. — Type: Brass 27827, Sudest I. [= Tagula], Mt Riu.

Glabrous except for the inflorescence and flowers shortly and sparsely tomentose. *Leaves* opposite; lamina lanceolate, 12–20 by 3–6 cm, shortly cuneate at the base to a petiole c. 3 mm long, acuminate and acute at the apex, glossy above, dull below; venation pinnate with the midrib prominent on both sides and other venation obscure. *Inflorescences* at the nodes, pedunculate c. 6-rayed umbels of tetrads with the outermost flower sessile and the lateral and inner ones pedicellate; peduncle c. 4 mm long; rays 3–4 mm long; pedicels of the lateral and inner-facing flowers 1–2 mm long. *Corolla* in mature bud 6-merous, c. 35 mm long, inflated at the base, weakly clavate and acute at the apex, pink; petals in the open flower coherent in the lower 10–12 mm. *Anther* c. 3 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: Papua New Guinea (Louiadiades Archipelago: Tagula I.).

Habitat & Ecology — 600–700 m altitude; no hosts recorded.

Note — Similar to *Amyema tetraflora*; for differences see Barlow, Blumea 36 (1992) 369.

8. *Amyema canaliculata* Barlow

Amyema canaliculata Barlow, Austral. J. Bot. 22 (1974) 569; in Handb. Fl. Papua New Guinea 2 (1981) 211; Blumea 36 (1992) 317. — Type: Henty & Foreman NGF 42624, Papua New Guinea, Prospect Creek.

Glabrous. *Leaves* scattered ternate; lamina linear-lanceolate, 7–13 by 0.3–0.6 cm, thick, convex below and strongly concave above, attenuate at the base to an obscure petiole c. 3 mm long, rounded and shortly mucronate at the apex, dull on both sides; venation invisible. *Inflorescences* at the nodes, pedunculate 3-rayed umbels of triads with all flowers sessile; peduncle c. 2 mm long; rays c. 4 mm long. *Corolla* in mature bud 5-merous, c. 24 mm long, uniformly slender, shortly rounded or obtuse at the apex, pink. Other floral characters unknown.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Known from type locality only, 600 m altitude; the recorded host is *Dacrydium*. Hosts other than dicotyledons are rare in *Loranthaceae*.

9. *Amyema caudiciflora* (Lauterb.) Danser

Amyema caudiciflora (Lauterb.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 294. — *Loranthus caudiciflorus* Lauterb., Nova Guinea 8 (1910) 290. — Type: *Versteeg 1473*, New Guinea, Irian Jaya, 'Noordrivier'.

[For additional synonymy see Barlow, *Blumea* 36 (1992) 318].

Glabrous. *Leaves* ternate, scattered ternate or quaternate; lamina usually ovate or ob-ovate (rarely lanceolate), (7–)12–21 by (3–)6–10 cm, cuneate or attenuate at the base and sessile or with a short thick petiole up to 3 mm long, often recurved at the margin, mostly rounded at the apex, dull on both sides; venation pinnate with the midrib distinct and raised below. *Inflorescences* at the nodes and along the internodes, pedunculate 4- to 6-rayed umbels of triads with all flowers sessile; peduncle (3–)10–15(–27) mm long; rays 5–9 mm long. *Corolla* in mature bud 5- or 6-merous, 27–35 mm long, uniformly slender, shortly rounded or obtuse at the apex, mostly pink, rarely red. *Anther* 2.5–4 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Highlands, in primary and secondary rain forest, mostly from 1250 to 2500 m altitude but occurring down to 500 m; recorded hosts include *Calophyllum*, *Castanopsis*, *Macaranga*, *Nothofagus*, *Opocunonia*.

Note — Closely related to *Amyema scandens*; for differences and species circumscription see Barlow, *Blumea* 36 (1992) 318.

10. *Amyema cauliflora* (Merr.) Barlow

Amyema cauliflora (Merr.) Barlow, *Blumea* 36 (1992) 319. — *Loranthus cauliflorus* Merr., Philipp. J. Sc. 1, Suppl. (1906) 105. — *Dicymanthes cauliflora* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 311. — Type: *Clemens 55*, Mindanao.

Glabrous. *Leaves* opposite; lamina ovate, up to 21 cm long, up to 8 cm wide, shortly cuneate at the base to a petiole up to 25 mm long, acuminate and acute at the apex, dull on both sides but darker above; venation pinnate with the midrib and the incurved main laterals prominent on both sides. *Inflorescences* at the nodes and along the internodes and epicortical runners, a head of 3 sessile flowers on a peduncle 1–2 mm long. *Corolla*

in mature bud 5- or 6-merous, 15–22 mm long, inflated at the base, weakly clavate and obtuse at the apex, angular, pink or red. *Anther* 4–6 mm long, sessile or nearly so.

Distribution — *Malesia*: Philippines (Mindanao).

Habitat & Ecology — Recorded once from 1000 m altitude; no host recorded.

Note — For discussion of equivalence of *Dicymanthes* and *Amyema*, see Barlow, *Blumea* 36 (1992) 298.

11. *Amyema celebica* (Tiegh.) Danser

Amyema celebica (Tiegh.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 294. — *Rhizanthemum celebicum* Tiegh. in Morot, J. de Bot. 15 (1901) 364. — Type: *Forsten 175*, Celebes, Tondano.

[For further synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 328; Philipp. J. Sc. 58 (1935) 80; Barlow, *Blumea* 36 (1992) 319].

Glabrous. *Leaves* mostly opposite, often scattered, sometimes quaternate; lamina lanceolate or elliptic to ovate, (6–)8–20 by (2–)4–7 cm, attenuate to truncate at the base to a petiole 10–20 mm long, obtuse to shortly acuminate and acute at the apex, dull on both sides, sometimes slightly darker above; venation pinnate with the midrib and the main laterals visible on both sides and prominent below. *Inflorescences* at the nodes and rarely on the epicortical runners, pedunculate (2–)4-rayed umbels of triads with all flowers pedicellate or rarely with the central flowers apparently sessile; peduncle (3–)10–25 (–50) mm long; rays (2–)5–10 mm long; pedicels (0–)2–4 mm long. *Corolla* in mature bud 5-merous, (15–)25–35 mm long, slender, acute at the apex, yellow, orange, red or purple, sometimes grading to green above. *Anther* 2–3.5 mm long, equal to or shorter than the free part of the filament. — **Fig. 3e.**

Distribution — *Malesia*: Philippines, Celebes, Lesser Sunda Islands (Sumba, Flores).

Habitat & Ecology — Mostly from 0 to 700 m but less frequently to 1900 m; no hosts recorded.

Note — Closely related to *Amyema acuta*; for differences and species circumscription see Barlow, *Blumea* 36 (1992) 307, 320.

12. *Amyema cercidioides* (K. Krause) Danser

Amyema cercidioides (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 294; Barlow, Austral. J. Bot. 22 (1974) 570; in Handb. Fl. Papua New Guinea 2 (1981) 211. — *Loranthus cercidioides* K. Krause, Nova Guinea 14 (1923) 103. — Type: *Lam 1893*, Irian Jaya, 'Doorman Top'.

Glabrous. *Leaves* opposite; lamina almost orbicular, 9–12 by 8–10 cm, cordate at the base, sessile, rounded at the apex, dull on both sides; venation pinnate with the midrib and the incurved main laterals distinct on both sides. *Inflorescences* at the nodes, pedunculate 3- or 4-rayed umbels of triads with all flowers sessile; peduncle c. 5 mm long; rays 6 mm long. *Corolla* in mature bud 6-merous, probably 24–27 mm long, not seen mature. *Anther* not seen mature, shorter than the free part of the filament.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Known only from the type collection from 1450 m altitude; no host recorded.

Note — Closely related to *Amyema caudiciflora*, differing in opposite leaves cordate at the base.

13. *Amyema conspicua* (F.M. Bailey) Danser

Amyema conspicua (F.M. Bailey) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 294; Barlow, Austral. J. Bot. 22 (1974) 571; in Handb. Fl. Papua New Guinea 2 (1981) 212. — *Loranthus conspicuus* F.M. Bailey, Queensl. Agric. J. 26 (1911) 198. — Type: *Bancroft s.n.*, Queensland, Eidsvold.

Glabrous except for the very young parts, inflorescences and ovaries white- or brown-tomentose. *Leaves* opposite; lamina oblong to ovate or obovate, 3–8 by 1–4.5 cm, attenuate to cuneate at the base to a petiole 1–6 mm long, rounded at the apex, dull on both sides; venation curvinerved, distinct on both sides. *Inflorescences* at the nodes, pedunculate 2-rayed umbels of triads with the central flowers sessile; peduncle (3–)4–8(–9) mm long; rays 1–2.5 mm long, densely tomentose above and glabrous or sparsely tomentose below; pedicels of the lateral flowers 0.5–1 mm long, with the same indumentum as the rays. *Corolla* in mature bud 4- or 5-merous, 14–25 mm long, slender, weakly clavate and acute at the apex, mostly green, rarely yellow or orange. *Anther* 1.5–2 mm long, about one fifth as long as the free part of the filament.

Distribution — Australia; *Malesia*: New Guinea.

Habitat & Ecology — See under the subspecies.

Notes — 1. There are 3 subspecies, of which 2 occur in Malesia. The external differences between these are probably not greater than the diversity within other polymorphic Malesian species; recognition of subspecies is more relevant in Australia, where ecogeographic divergence in open communities across a large land area is more striking, and may reflect stronger differentiation of gene pools.

2. The species is one of the relatively few loranth in Malesia which lacks epicortical runners.

KEY TO THE SUBSPECIES

- 1a. Indumentum white; leaves widest at or below the middle, not recurved at the margin a. subsp. **conspicua**
- b. Indumentum brown, mixed with white on the ovary; leaves widest above the middle, recurved at the margin b. subsp. **fulvicalyx**

a. subsp. **conspicua**

Distribution — Eastern Australia; *Malesia*: Papua New Guinea, Gulf Province.

Habitat & Ecology — In Australia known from coastal districts, in open and closed forests, parasitic on many hosts, including mangroves, but common on *Alphitonia*. In New Guinea known only from mangrove communities; the only recorded host is *Avicennia*.

b. subsp. *fulvicalyx* Barlow

Amyema conspicua (F.M. Bailey) Danser subsp. *fulvicalyx* Barlow, Austral. J. Bot. 22 (1974) 573. — Type: *Barlow 951*, Papua New Guinea, Wau.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Disturbed forests, 1200–1800 m; no hosts recorded.

14. *Amyema corniculata* Danser

Amyema corniculata Danser, Brittonia 2 (1936) 133; Barlow, Austral. J. Bot. 22 (1974) 573; in Handb. Fl. Papua New Guinea 2 (1981) 212. — Type: *Brass 4564*, Papua New Guinea, Murray Pass.

Glabrous. *Leaves* opposite; lamina ovate to nearly orbicular, 2–4 by 1.8–2.5 cm, shortly cuneate at the base to a petiole 2–4 mm long, rounded at the apex, glossy above, dull below; venation pinnate with only the midrib faintly visible. *Inflorescences* at the nodes, pedunculate 4-rayed umbels of triads with the central flowers sessile; peduncle 19–26 mm long, very slender; rays 3–4 mm long, spreading, thicker than the peduncle; pedicels of the lateral flowers c. 2 mm long; bracts with complex dorsal protuberances. *Corolla* in mature bud 4-merous, 16–18 mm long, very slender, weakly clavate and acute at the apex, red. *Anther* c. 1 mm long, about one third as long as the free part of the filament.

Distribution — *Malesia*: New Guinea, known only from Mt Albert Edward in Papua New Guinea.

Habitat & Ecology — Subalpine forests, 2840 m altitude; no hosts recorded.

Note — Closely related to other subalpine *Amyema* species in New Guinea; for differences see Barlow, Austral. J. Bot. 22 (1974) 573; Blumea 36 (1992) 323.

15. *Amyema cuernosensis* (Elmer) Barlow

Amyema cuernosensis (Elmer) Barlow, Blumea 36 (1992) 323. — *Loranthus cuernosensis* Elmer, Leaf. Philipp. Bot. 2 (1908) 469. — *Dicymanthes cuernosensis* (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 311. — Type: *Elmer 9525*, lecto, Philippines, Negros. *Dicymanthes breviflora* Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 363; Backer & Bakh. f., Fl. Java 2 (1965) 71. — Type: *Forsten s.n.*, Celebes, Tondano. *Dicymanthes lombocana* Danser, Blumea 2 (1936) 58. — Type: *Elbert 1700*, Lombok, Mt Rindjani.

Glabrous or the inflorescence and flowers sparsely brown-tomentose. *Leaves* opposite; lamina elliptic to ovate, 6–20 by 3–8 cm, truncate to cordate at the base, sessile, usually weakly acuminate and acute at the apex, grey and often glossy above, dull brown below; venation pinnate with the midrib prominent towards the base and the main laterals visible on both sides. *Inflorescences* at the nodes; a subsessile 6-flowered head of 2 sessile triads on a short or obscure peduncle 0.5–1.5(–2.5) mm long. *Corolla* in mature bud 5-merous, (12–)17–23 mm long, slender, very weakly clavate and acute or obtuse at the apex, yellow to red, sometimes paler below. *Anther* (1–)2.5–4 mm long, usually about equal to the free part of the filament.

Distribution — *Malesia*: Java, Philippines, Celebes, Lesser Sunda Islands (Bali, Lombok, Flores).

Habitat & Ecology — 800–1800 m altitude; the only recorded host is *Lantana*.

Notes — 1. Related to *Amyema edanoi*; for differences see Barlow, Blumea 36 (1992) 324.

2. For discussion of equivalence of *Dicymanthes* and *Amyema*, see Barlow, Blumea 36 (1992) 298.

16. *Amyema curranii* (Merr.) Danser

Amyema curranii (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 294. — *Loranthus curranii* Merr., Philipp. J. Sc., Bot. 4 (1909) 144. — Type: Curran FB 5035, holo, Luzon, Mt Santo Tomas; Jacobs 7578, neo, Luzon, Mt Tabayoc.

Glabrous except for the inflorescences and flowers shortly tomentose. *Leaves* ternate or scattered ternate; lamina narrowly ovate, 5–18 by 1.5–5 cm, shortly cuneate from the rounded base to a petiole 5–18 mm long, shortly acuminate and acute at the apex, glossy above, dull below; venation pinnate with the midrib prominent below and the midrib and main laterals distinct above. *Inflorescences* at the nodes, pedunculate 18- to 40-rayed umbels of triads with the central flowers sessile or very shortly pedicellate and the lateral flowers pedicellate; peduncle 6–13 mm long, dilated at the apex; rays 3–4 mm long; pedicels of the central flowers 0–0.3 mm long, of the lateral flowers 0.5–1.5 mm long. *Corolla* in mature bud 4-merous, 30–35 mm long, slender, clavate and obtuse at the apex, red. *Anther* 2–3 mm long, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — 1200–2400 m altitude; no hosts recorded.

Note — Similar to *Amyema incarnatiflora*, differing in its variably pedicellate 4-merous flowers.

17. *Amyema dilatipes* Barlow

Amyema dilatipes Barlow, Austral. J. Bot. 22 (1974) 575; in Handb. Fl. Papua New Guinea 2 (1981); Van Royen, Alpine Fl. New Guinea 3 (1982) 2264. — Type: Brass 30053, Papua New Guinea, Mt Wilhelm.

Glabrous. *Leaves* ternate or quaternate; lamina narrowly ovate to elliptic, (2–)4–7 by 1.2–3 cm, shortly cuneate at the base to a petiole (2–)4–6 mm long, acute at the apex, glossy above, dull below; venation pinnate with the midrib distinct on both sides and the main laterals visible above. *Inflorescences* at the nodes and on the epicortical runners, pedunculate 14- to 22-rayed umbels of tetrads with the central flowers sessile; peduncle mostly 30–70 mm long, dilated up to 7 mm wide at the apex; rays 7–11 mm long; pedicels of the lateral flowers 3–5 mm long; bracts variously lobed, branched or twisted. *Corolla* in mature bud 4-merous, 25–40 mm long, slender, clavate and acute to rounded at the apex, red or orange. *Anther* 2–3 mm long, about equal to the free part of the filament. — **Fig. 5d, e.**

Distribution — *Malesia*: Papua New Guinea (Eastern Highlands Province).

Habitat & Ecology — Subalpine communities from 3300 to 3750 m altitude; recorded hosts include *Eurya* and *Rapanea*.

Note — For a discussion of apparent phantom hybrids, see Barlow, *Blumea* 36 (1992) 326.

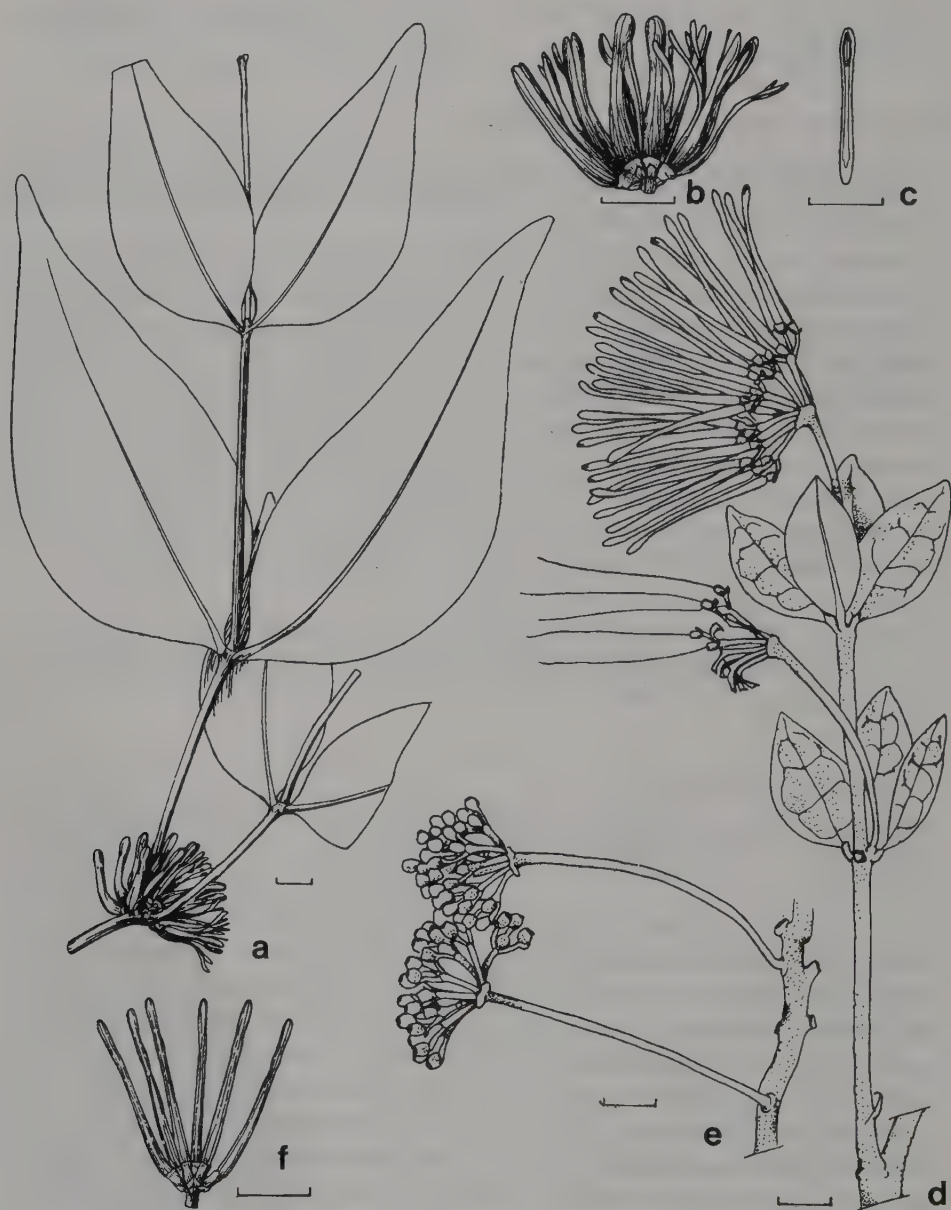


Fig. 5. *Amyema edanoi* (Merr.) Barlow. a. Flower-bearing twig; b. inflorescence; c. section of flower bud. — *A. dilatipes* Barlow. d. Flower-bearing twig; e. inflorescences with young fruit. — *A. hexameres* (Danser) Barlow. f. Inflorescence (a–e: not cited; f: *Lam* 3621). a–c Redrawn from Danser (1935); d, e redrawn from Barlow (1981); f redrawn from Danser (1931). Scale bars represent 1 cm.

18. *Amyema edanoi* (Merr.) Barlow

Amyema edanoi (Merr.) Barlow, *Blumea* 36 (1992) 328. — *Loranthus edanoi* Merr., *Philipp. J. Sc., Bot.* 13 (1918) 275. — *Dicymanthes edanoi* (Merr.) Danser, *Bull. Jard. Bot. Buitenzorg* III, 10 (1929) 311. — Type: *Ramos & Edaño BS 26241*, lecto, Luzon, Mt Umingan.
[For additional synonymy see Barlow, *Blumea* 36 (1992) 328].

Glabrous or the inflorescence and flowers sparsely brown tomentose. *Leaves* opposite; lamina narrowly ovate to ovate, 9–15(–22) by 4.5–7(–11) cm, shortly cuneate to slightly cordate at the base, sessile, weakly acuminate and acute at the apex, dull on both sides; venation pinnate with the midrib and the main laterals visible on both sides. *Inflorescences* at the nodes, a 6-flowered head of 2 sessile triads on a peduncle 2–6 mm long. *Corolla* in mature bud 5-merous, 11–16(–23) mm long, slender, weakly clavate and acute at the apex, red or yellowish brown. *Anther* mostly c. 2.5 mm long, usually longer than the free part of the filament. — **Fig. 5a–c.**

Distribution — *Malesia*: Philippines, Celebes.

Habitat & Ecology — Humid forests from 0 to 1000 m altitude; recorded hosts include *Ficus* and *Zanthophyllum*.

Notes — 1. Related to *Amyema cuernosensis*; for differences see there.

2. For discussion of equivalence of *Dicymanthes* and *Amyema*, see Barlow, *Blumea* 36 (1992) 298.

19. *Amyema enneantha* Barlow

Amyema enneantha Barlow, *Blumea* 36 (1992) 329. — Type: *Kostermans & Wirawan 706*, Flores, Mt Ranaka.

Glabrous. *Leaves* ternate; lamina narrowly ovate, 8–15 by 3.5–6 cm, attenuate at the base to an obscure petiole 0–5 mm long, shortly acuminate and acute at the apex, dark grey and glossy above, dull brown below; venation pinnate, obscure except for the midrib prominent and raised towards the base on both sides. *Inflorescences* at the nodes, a subsessile 9-flowered head of 3 sessile triads on a very short or obscure peduncle 0.5–1 mm long. *Corolla* in mature bud 5-merous, 22–30 mm long, moderately robust, almost cylindrical, obtuse at the apex, pink or red, sometimes white below. *Anther* 3–4.5 mm long, usually slightly longer than the free part of the filament.

Distribution — *Malesia*: Lesser Sunda Islands (Flores).

Habitat & Ecology — 1500–2400 m altitude; no hosts recorded.

Note — Related to *Amyema cuernosensis*. For discussion of differences from this species and the equivalence of *Dicymanthes* and *Amyema*, see Barlow, *Blumea* 36 (1992) 298, 330.

20. *Amyema fasciculata* (Blume) Danser

Amyema fasciculata (Blume) Danser, *Bull. Jard. Bot. Buitenzorg* III, 10 (1929) 295; Backer & Bakh. f., *Fl. Java* 2 (1965) 71; Barlow, *Blumea* 36 (1992) 330. — *Loranthus fasciculatus* Blume, *Bijdr.* (1826) 661. — Type: *Blume s.n.*, Java, Mt Ceremai.

Amyema aquilonia Danser, Philipp. J. Sc. 58 (1935) 86. — Type: *Ramos BS 33296*, Luzon, Mt Palimlim.

Amyema apoda Barlow, Austral. J. Bot. 22 (1974) 565; in Handb. Fl. Papua New Guinea 2 (1981) 209. — Type: *Pleyte 708*, Irian Jaya, Sorong.

[For guide to further synonymy see Barlow, *Blumea* 36 (1992) 330].

Glabrous or the young inflorescence and flowers tomentose. *Leaves* opposite, ternate or quaternate; lamina very variable, narrowly elliptic to obovate, (3–)5–10(–20) by 1–4(–12) cm, attenuate at the base to a winged petiole obscure or up to 20 mm long, usually obtuse at the apex, dull on both sides or somewhat lustrous above; venation pinnate with the midrib distinct towards the base. *Inflorescences* at the nodes and along the internodes, simple 2- to 4-flowered umbels; peduncle slender, 1–6 mm long; rays (0.5–) 2–3 mm long. *Corolla* in mature bud 4- or rarely 5-merous, 14–18 mm long, rather slender, obtuse at the apex, mostly red or violet below and green above. *Anther* 2–2.5 mm long, much longer than the free part of the filament. — **Fig. 9e, f.**

Distribution — *Malesia*: Philippines, Borneo and Java southeastwards to Bird's Head Peninsula in New Guinea.

Habitat & Ecology — 0–1500 m altitude; no hosts recorded.

Note — The species can be confused with *Amyema beccarii*; for discussion see Barlow, *Blumea* 36 (1992) 314.

21. *Amyema finisterrae* (Warb.) Danser

Amyema finisterrae (Warb.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 295; Barlow in Handb. Fl. Papua New Guinea 2 (1981) 213; Van Royen, Alpine Fl. New Guinea 3 (1982) 2259. — *Loranthus finisterrae* Warb., Bot. Jahrb. 16 (1893) 20. — Type: *Hellwig 322*, Papua New Guinea, Finisterre Mts.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 332; Barlow, Austral. J. Bot. 22 (1974) 576].

Glabrous. *Leaves* opposite; lamina oblong to elliptic or spatulate, 1.8–4(–6) by 1.5–3 cm, cuneate at the base to a petiole 4–7 mm long, mostly rounded (rarely acuminate and acute) at the apex, dull on both sides or somewhat lustrous above, recurved at the margins; venation pinnate with the midrib usually visible and the main laterals diverging near the base. *Inflorescences* at the nodes, a single pedicellate flower on a slender ebracteate peduncle 2–4(–6) mm long (i.e., a flower on a jointed 'pedicel'); pedicel 1.5–3 mm long, slender, wider at the apex, usually with a single bract. *Corolla* in mature bud 4-merous, (13–)20–35 mm long, quadrangular, sometimes winged, acute or obtuse at the apex, mostly dark pink, red or purple, often paler or shading to yellow or green above. *Anther* 2–3 mm long, about half as long as the free part of the filament. — **Fig. 6c.**

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Primary and secondary humid forests, 1300–2600 m altitude; recorded hosts include *Acalypha*, *Aglaia*, *Castanopsis*, *Dimorphanthera*, *Dodonaea*, *Ficus*, and *Glochidion*.

Note — For discussion of inflorescence structure and comparison with the related *Amyema hastifolia*, see Barlow, *Blumea* 36 (1992) 332.

22. *Amyema friesiana* (K. Schum.) Danser

Amyema friesiana (K. Schum.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 295; Barlow, Austral. J. Bot. 22 (1974) 577; in Handb. Fl. Papua New Guinea 2 (1981) 215. — *Loranthus friesianus* K. Schum. in K. Schum. & Lauterb., Nachtr. Fl. Deutsch. Schutzgeb. Südsee (1905) 258. — Type: *Nyman 41*, lecto, Papua New Guinea, 'Stephansort'.

Glabrous except for the inflorescences and flowers sparsely to densely white- or brown-tomentose. *Leaves* opposite; lamina lanceolate to broadly ovate, often falcate or oblique, (6–)8–15(–20) by 3–7(–10) cm, shortly cuneate at the base to a petiole (8–)10–20(–30) mm long, mostly acuminate and acute at the apex, dull on both sides; venation nearly curvinerved, distinct on both sides. *Inflorescences* at the nodes, pedunculate 5- to 8-rayed umbels of triads with all flowers sessile; peduncle 18–30 mm long; rays 5–10 mm long. *Corolla* in mature bud 6-merous, 28–35 mm long, slender, weakly clavate and acute or obtuse or rounded at the apex, orange or red, often paler or shading to yellow or green above. *Anther* 2.5–3 mm long, about 3 times as long as the free part of the filament. — **Fig. 8c, d.**

Distribution — Australia (Cape York Peninsula); *Malesia*: New Guinea.

Habitat & Ecology — Primary and secondary humid forests at 0–2600 m altitude but mostly at 1500–2000 m; recorded hosts include *Acalypha*, *Callicarpa*, *Elaeocarpus*, *Ficus*, *Geunsia*, *Macaranga*, *Nauclea*, *Nothofagus* and commonly *Homalanthus*.

Note — For discussion of species distinction within the *Amyema scandens* complex, see Barlow, Blumea 36 (1992) 333, 363, 371.

23. *Amyema gravis* Danser

Amyema gravis Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 336; Backer & Bakh. f., Fl. Java 2 (1965) 71. — Type: *van Steenis 2645*, lecto, Java, Pasuruan.

Glabrous. *Leaves* opposite; lamina obovate, 2.5–5 by 1.5–3 cm, shortly cuneate to truncate at the base to a petiole mostly 3–5 mm long, rounded at the apex, thick, dull on both sides; venation indistinct. *Inflorescences* at the nodes, pedunculate 2- to 5-rayed umbels of triads with the central flowers sessile; peduncle (3–)6–18(–22) mm long; rays 3–6 mm long; pedicels of the lateral flowers 1–2 mm long. *Corolla* in mature bud 4-merous, 28–30 mm long, inflated at the base, clavate and obtuse at the apex, yellowish green below and red above. *Anther* c. 4 mm long, transversely septate, slightly longer than the free part of the filament.

Distribution — *Malesia*: Borneo, Java.

Habitat & Ecology — Maritime communities, parasitic on mangroves, recorded on *Avicennia*, *Rhizophora*, and *Sonneratia*.

Note — For comparison with other mistletoe parasites of mangroves, see Barlow, Blumea 36 (1992) 335.

24. *Amyema haenkeana* (Schult. & Schult. f.) Danser

Amyema haenkeana (Schult.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 295. — *Loranthus haenkeanus* Schult. & Schult. f., Syst. Veg. 7, 1 (1828) 113. — Type: *Haenke s.n.*, Philippines. [For additional synonymy see Danser, Philipp. J. Sc. 58 (1935) 63].

Glabrous except for a dense tawny tomentum on the inflorescence and flowers. *Leaves* opposite or ternate, usually scattered; lamina lanceolate or narrowly ovate, 8–22 (–30) by 1–7 (–12) cm, shortly cuneate to slightly cordate at the base to a petiole 10–25 mm long, somewhat acuminate but finally obtuse or rounded at the apex, dull on both sides or slightly lustrous above; venation pinnate with the midrib prominent below. *Inflorescences* at the nodes and on the epicortical runners, pedunculate 30- to 50-rayed umbels of triads with the central flowers mostly sessile; peduncle (10–)20–50 mm long, dilated at apex; rays 5–10 mm long; pedicels of the lateral flowers 1–2 mm long. *Corolla* in mature bud 5- or 6-merous, 30–38 mm long, slightly dilated at the base, clavate and obtuse at the apex, mostly red, rarely yellow; petals shortly coherent at the base after anthesis. *Anther* 1–4 mm long, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Philippines.

Habitat & Ecology — 0–450 m altitude; no hosts recorded.

25. *Amyema halconensis* (Merr.) Danser

Amyema halconensis (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 296. — *Loranthus halconensis* Merr., Philipp. J. Sc., Bot. 2 (1907) 271. — Type: *Merrill 5664*, lecto, Mindoro, Mt Halcon. [For additional synonymy see Danser, Philipp. J. Sc. 58 (1935) 69].

Glabrous except for the inflorescences and flowers sparsely to densely white- or pale brown-tomentose. *Leaves* in whorls of 3–8; lamina lanceolate to oblong, 10–21 by 2–8 cm, shortly cuneate at base to a petiole 8–20 mm long, usually acuminate and acute at apex, glossy above, dull below; venation pinnate, distinct above and the midrib prominent for its full length below. *Inflorescences* at the nodes and on the epicortical runners, pedunculate 6- to 8-rayed umbels of triads with all flowers variably pedicellate; peduncle 3–7 mm long; rays 1–3 mm long; pedicels 0.5–1.5 mm long, rarely obsolete. *Corolla* in mature bud (4–)5(–6)-merous, 22–33 mm long, slightly dilated in the lower part, weakly clavate and acute at apex, yellow; petals long coherent after anthesis, especially in the lower 1–2 mm. *Anther* 2–3 mm long, about equal to the free part of the filament.

Distribution — *Malesia*: Philippines.

Habitat & Ecology — Lowlands, only recorded from 0 to 100 m altitude; no hosts recorded.

Note — For species distinction within the *Amyema polytrias* species group, see Barlow, Blumea 36 (1992) 356.

26. *Amyema hastifolia* (Ridl.) Danser

Amyema hastifolia (Ridl.) Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 337; Barlow, Austral. J. Bot. 22 (1974) 577; in Handb. Fl. Papua New Guinea 2 (1981) 215. — *Loranthus hastifolius* Ridl., Trans. Linn. Soc. Bot. 9 (1916) 146. — *Rhizomonanthes hastifolia* (Ridl.) Danser, Verh. Kon. Ned. Akad. Wet. Amst. Afd. Natuurk., Sect. 2, 29 (1933) 101. — Type: *Kloss s.n.*, New Guinea, Irian Jaya, Nassau Mts.

Loranthus curvifolius & *heterochromus* K. Krause, Bot. Jahrb. 57 (1922) 465. — *Amyema curvifolia* & *heterochroma* (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1929) 330, 337; Barlow, Austral. J. Bot. 22 (1974) 574. — Types: *Ledermann 13077* & *12569*, New Guinea, 'Felsspitze'.

Glabrous except for the inflorescence and ovary thinly tomentose. *Leaves* opposite; lamina elliptic to ovate, 4–7 by 2–5 cm, shortly cuneate at the base to a petiole c. 2 mm long, shortly acuminate and acute at the apex, lustrous above, dull below; venation pinnate but almost curvinerved, with the midrib distinct on both sides and the main laterals distinct above. *Inflorescences* at the nodes, along the internodes and on the epicortical runners, a single pedicellate flower on a slender ebracteate peduncule about 2 mm long (i. e., a flower on a jointed 'pedicel'); pedicel 0.5–1 mm long, funnel-shaped, with a single bract. *Corolla* in mature bud 4-merous, c. 40 mm long, quadrangular, acute at the apex, mostly red below and paler red or yellow above. *Anther* c. 5 mm long, about equal to the free part of the filament. — **Fig. 6a, b.**

Distribution — *Malesia*: New Guinea (Irian Jaya).

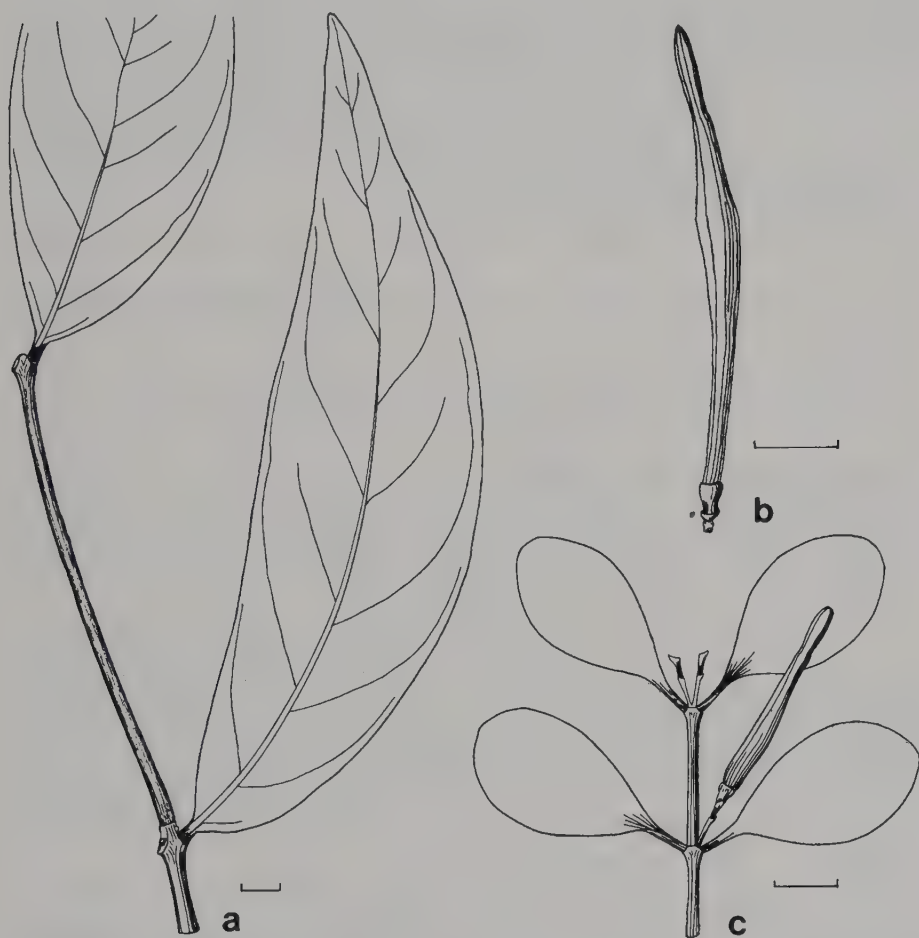


Fig. 6. *Amyema hastifolia* (Ridl.) Danser. a. Twig with leaves; b. flower bud. — *A. finisterrae* (Warb.) Danser. c. Twig with leaves and flowers (a, b: *Ledermann 13077*; c: *Hellwig 322*). Redrawn from Danser (1931). Scale bars represent 1 cm.

Habitat & Ecology — Highlands, 1250–2800 m altitude; no hosts recorded.

Note — For discussion of inflorescence structure, comparison with the related *Amyema finisterrae*, and synonymy of *Amyema curvifolia* see Barlow, Blumea 36 (1992) 332, 338.

27. *Amyema hexameres* (Danser) Barlow

Amyema hexameres (Danser) Barlow, Blumea 36 (1992) 339. — *Dicymanthes hexameres* Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 364. — Type: *Lam 3621*, Moluccas, Guguti.

Glabrous except for the ovary and sometimes the corolla shortly and sparsely brown-tomentose. *Leaves* opposite; lamina elliptic to ovate, 8–15 by 5–7.5 cm, truncate and finally shortly cuneate at the base to a petiole 5–10 mm long, obtuse or broadly acute at the apex, glossy grey-green above, dull brown below; venation pinnate with the midrib raised below and the main laterals visible. *Inflorescences* at the nodes and on the epicortical runners, a 6-flowered head of 2 sessile triads on a peduncle (0.5–)2–2.5 mm long. *Corolla* in mature bud 5-merous, 20–25 mm long, relatively slender, weakly clavate and acute, pink or red and sometimes yellow above. *Anther* 2.5–4 mm long, usually slightly longer than the free part of the filament. — **Fig. 5f.**

Distribution — *Malesia*: Northern Moluccas.

Habitat & Ecology — Probably in humid forests, 0–1050 m altitude; no hosts recorded.

Notes — 1. Similar to *Amyema hexantha*; for differences see Barlow, Blumea 36 (1992) 340.

2. For discussion of equivalence of *Dicymanthes* and *Amyema*, see Barlow, Blumea 36 (1992) 298.

28. *Amyema hexantha* (Merr.) Barlow

Amyema hexantha (Merr.) Barlow, Blumea 36 (1992) 340. — *Loranthus hexanthus* Merr., Philipp. J. Sc., Bot. 4 (1909) 137. — *Dicymanthes hexantha* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 311. — Type: *Williams 2565*, lecto, Mindanao, Mt Apo.

Glabrous. *Leaves* opposite; lamina mostly ovate, 6–18 by 3–9 cm, cuneate at the base to a petiole 5–10 mm long, acuminate and obtuse at the apex, dull on both sides but slightly darker above; venation pinnate with the midrib prominent below and the midrib and main laterals visible above. *Inflorescences* at the nodes, a 6-flowered head of 2 sessile triads on a peduncle 3–5 mm long. *Corolla* in mature bud 5-merous, c. 17 mm long, slightly inflated at the base, clavate and obtuse at the apex, angular in the upper part, red. *Anther* 2–2.5 mm long, about equal to the free part of the filament.

Distribution — *Malesia*: Philippines (Mindanao).

Habitat & Ecology — 850–1800 m altitude; no hosts recorded.

Notes — 1. Similar to *Amyema hexameres*; for differences see Barlow, Blumea 36 (1992) 340.

2. For discussion of equivalence of *Dicymanthes* and *Amyema*, see Barlow, Blumea 36 (1992) 298.

29. *Amyema incarnatiflora* (Elmer) Danser

Amyema incarnatiflora (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 296. — *Loranthus incarnatiflorus* Elmer, Leaflet Philipp. Bot. 6 (1913) 1969. — Type: *Elmer 11817*, lecto, Mindanao, Mt Apo.

[For additional synonymy see Danser, Philipp. J. Sc. 58 (1935) 70].

Glabrous except for the inflorescence and ovary white-tomentose and the corolla sparsely so. *Leaves* opposite or ternate, frequently scattered; lamina lanceolate to ovate, 5–12 by 2–6.5 cm, shortly cuneate to weakly cordate at the base to a petiole 5–25 mm long, mostly acuminate and acute at the apex, dull on both sides; venation pinnate with the midrib visible above and prominent below. *Inflorescences* at the nodes and on the epicortical runners, pedunculate 10- to 30-rayed umbels of triads with all flowers sessile; peduncle 8–25 mm long, dilated at the apex; rays 1–6 mm long. *Corolla* in mature bud 5-merous, 25–30 mm long, slightly dilated at the base, clavate and obtuse at the apex, pink or red and sometimes shading to green above. *Anther* 1.5–2.5 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: Philippines.

Habitat & Ecology — 0–1725 m altitude; no hosts recorded.

Note — Similar to *Amyema curranii*, which differs in its variably pedicellate 4-merous flowers.

30. *Amyema irrubescens* Barlow

Amyema irrubescens Barlow, Blumea 36 (1992) 342. — Type: *van Balgooy 3326*, Celebes, Mt Roroka Timbu.

Glabrous. *Leaves* opposite, ternate or scattered; lamina ovate, 6–9 by 3–4.5 cm, attenuate at the base to a petiole 4–8 mm long, broadly acute or obtuse at the apex, dark and glossy above, dull below; venation pinnate with the midrib prominent below. *Inflorescences* at the nodes and along the internodes, pedunculate 9- to 11-rayed umbels of triads with all flowers shortly pedicellate; peduncle 11–16 mm long; rays 3–4.5 mm long; pedicels 0.5–1.5 mm long or sometimes obsolete. *Corolla* in mature bud 4-merous, c. 32 mm long, slender, weakly clavate and acute at the apex. *Anther* 2.5–3 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: Celebes.

Habitat & Ecology — Known from two collections at 2450 m altitude; recorded as parasitic on *Phyllocladus*. Hosts other than dicotyledons are rare in *Loranthaceae*.

Note — For species distinction within the *Amyema polytrias* species group, see Barlow, Blumea 36 (1992) 343, 356.

31. *Amyema kebarensis* Barlow

Amyema kebarensis Barlow, Austral. J. Bot. 22 (1974) 579; in Handb. Fl. Papua New Guinea 2 (1981) 216. — Type: *van Royen & Sleumer 8256*, Irian Jaya, Kebar Valley.

Glabrous except for a few scattered hairs on the inflorescences and flowers. *Leaves* opposite; lamina narrowly lanceolate, 4–7 cm long, mostly 0.4–0.7 cm wide, attenuate

at the base to a petiole 1–3 mm long, acuminate and acute at the apex, dull on both sides, often rolled when dry; venation obscure. *Inflorescences* at the nodes, pedunculate 3- or 4-rayed umbels of triads with the central flowers sessile; peduncle mostly 8–15 mm long, slender; rays c. 8 mm long, slender, wider towards the apex; pedicels of the lateral flowers 2–3 mm long. *Corolla* in mature bud 4-merous, c. 18 mm long, very slender, rounded at the apex, red or purple below and green or yellow above. *Anther* c. 2 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: New Guinea (Bird's Head Peninsula).

Habitat & Ecology — 700–2100 m altitude; recorded hosts include *Clethra*, *Vaccinium*, and *Trochocarpa*.

32. *Amyema longipes* (Danser) Barlow

Amyema longipes (Danser) Barlow, *Blumea* 36 (1992) 344. — *Dicymanthes longipes* Danser, *Bull. Jard. Bot. Buitenzorg* III, 11 (1931) 365. — Type: *Sarip* 377, Bali, Mt Batukau.

Glabrous. *Leaves* opposite; lamina ovate to obovate, 3–8 by 2–5 cm, attenuate to shortly cuneate at the base to a petiole 2–7 mm long, obtuse or rounded at the apex, dull on both sides but slightly darker above; venation pinnate with the midrib prominent below and the other veins obscure. *Inflorescences* at the nodes, a 6-flowered head of 2 sessile triads on a peduncle 5–11 mm long. *Corolla* in mature bud 5-merous, 20–23 mm long, rather slender, not clavate, acute at the apex, red. *Anther* c. 2 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: Bali.

Habitat & Ecology — 1600–1935 m altitude; no hosts recorded.

Notes — 1. Similar to *Amyema hexantha*; for differences see Barlow, *Blumea* 36 (1992) 344.

2. For discussion of equivalence of *Dicymanthes* and *Amyema*, see Barlow, *Blumea* 36 (1992) 298.

33. *Amyema luzonensis* (Schult. & Schult. f.) Danser

Amyema luzonensis (Schult. & Schult. f.) Danser, *Bull. Jard. Bot. Buitenzorg* III, 10 (1929) 296. — *Loranthus luzonensis* Schult. & Schult. f., *Syst. Veg.* 7, 1 (1829) 104. — Type: *Haenke s.n.*, Philippines.

[For additional synonymy see Danser, *Philipp. J. Sc.* 58 (1935) 72; Barlow, *Blumea* 36 (1992) 345].

Glabrous except for the inflorescence and flowers sparsely tomentose. *Leaves* quaternate; lamina oblong to obovate, 1–6 by 0.8–2 cm, truncate or rounded at the base, sessile, rounded at the apex, glossy above, dull below; venation pinnate with the midrib and the main laterals faintly visible above and the midrib prominent below. *Inflorescences* at the nodes, pedunculate mostly 4-rayed umbels of triads usually with all flowers pedicellate but sometimes with the central flowers and very rarely the lateral flowers sessile; peduncle 7–30 mm long; rays 1–4 mm long; pedicels 0–2 mm long. *Corolla* in mature bud 4-merous, 25–38 mm long, gradually inflated to 3/4 of its length, thence attenuate

to an acute apex, red orange or yellow below, sometimes shading to green above. *Anther* 2–4 mm long, longer than the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — 0–900 m altitude; no hosts recorded.

Note — Closely related to *Amyema benguetensis* and *A. rhytidoderma*; for discussion see Barlow, *Blumea* 36 (1992) 314, 345.

34. *Amyema mackayensis* (Blakely) Danser

Amyema mackayensis (Blakely) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 297; Barlow in Handb. Fl. Papua New Guinea 2 (1981) 216. — *Loranthus mackayensis* Blakely, Proc. Linn. Soc. New S Wales 47 (1922) 392; 48 (1923) 131. — Type: *Tryon s.n.*, Queensland, Mackay.
[For additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 580; *Blumea* 36 (1992) 345].

Glabrous except for the ovary very rarely sparsely brown-tomentose. *Leaves* opposite; lamina elliptic to orbicular, mostly 2.5–5 cm long, mostly 1.5–4 cm wide, cuneate at the base to a petiole 3–6 mm long, rounded at the apex, thick, dull on both sides; venation curvinerved, obscure. *Inflorescences* at the nodes, pedunculate mostly 3- or 4-rayed umbels of triads with the central flowers sessile; peduncle 6–22 mm long; rays 4–10 mm long; pedicels of the lateral flowers 2–5 mm long. *Corolla* in mature bud 5-merous, 10–28 mm long, slender, clavate and obtuse at the apex, red, yellow or green, sometimes paler above. *Anther* 1.5–3 mm long, about half as long as the free part of the filament.

Distribution — Northern Australia; *Malesia*: southern New Guinea.

Habitat & Ecology — Exclusively in mangrove communities; recorded as parasitic on *Avicennia*, *Camptostemon*, *Ceriops*, *Excoecaria*, *Lumnitzera*, *Rhizophora*, and *Sonneratia*.

Notes — 1. For discussion of status of former subspecies, see Barlow, *Blumea* 36 (1992) 346.

2. The species is one of the relatively few loranth in *Malesia* which lacks epicortical runners.

35. *Amyema miraculosa* (Miq.) Tiegh.

Amyema miraculosa (Miq.) Tiegh., Bull. Soc. Bot. France 42 (1895) 83, 84. — *Loranthus miraculosus* Miq. in Lehm., Pl. Preiss. 1 (1845) 281. — Type: *Preiss 1609*, Western Australia, Wicklow.
[For additional synonymy see Barlow in Fl. Australia 22 (1984) 98, 99].

Glabrous except for the ovary and young vegetative parts very rarely sparsely tomentose. *Leaves* opposite; lamina lanceolate to elliptic or obovate-spathulate, 2.5–10 by 0.5–3 cm, attenuate or cuneate at the base to a petiole 2–10 mm long, acute to rounded at the apex, dull on both sides; venation curvinerved, distinct on both sides. *Inflorescences* at the nodes, pedunculate 2- or 3-rayed umbels of triads with the central flowers sessile; peduncle 6–30 mm long; rays 3–10 mm long; pedicels of the lateral flowers 1.5–7 mm long. *Corolla* in mature bud 4- or 5-merous, 8–25 mm long, slender, clavate and obtuse at the apex, ridged or winged in the upper part, red, mostly very dark below

and paler above. *Anther* 1–2 mm long, about one quarter as long as the free part of the filament.

Distribution — Australia; *Malesia*: Timor.

Habitat & Ecology — See under the subspecies.

Notes — 1. There are 3 subspecies, of which 1 occurs in Malesia. The differences between these are possibly not greater than the diversity within other polymorphic Malesian species; recognition of subspecies is more relevant in Australia, where ecogeographic divergence in open communities across a large land area is more striking, and may reflect stronger differentiation of gene pools.

2. The species is one of the relatively few loranth in Malesia which lacks epicortical runners.

subsp. **latifolia** Barlow

Amyema miraculosa (Miq.) Tiegh. subsp. *latifolia* Barlow, *Blumea* 36 (1992) 350. — Type: *Forbes* 3543, Timor.

Leaf lamina lanceolate-spathulate, 5–8 by 2–3 cm, thin, attenuate at the base to a petiole c. 5 mm long. *Inflorescence* peduncle c. 20 mm long, deflexed; rays 3, c. 5 mm long, pedicels of the lateral flowers c. 2.5 mm long. *Corolla* 20–25 mm long, purple.

Distribution — *Malesia*: Timor.

Habitat & Ecology — Probably open woodlands; the only host record is *Pittosporum*.

Note — For discussion of relationship with Australian subspecies, see Barlow, *Blumea* 36 (1992) 350.

36. *Amyema novaebritanniae* (K. Schum.) Danser

Amyema novaebritanniae (K. Schum.) Danser, *Bull. Jard. Bot. Buitenzorg* III, 10 (1929) 297; Barlow, *Austral. J. Bot.* 22 (1974) 581; in *Handb. Fl. Papua New Guinea* 2 (1981) 217. — *Loranthus novaebritanniae* K. Schum. in K. Schum. & Lauterb., *Nachr. Fl. Deutsch. Schutzgeb. Südsee* (1905) 259. — Type: *Schlechter* 13765, New Britain.

Loranthus jambosae G.M. Schulze, *Notizbl. Berl.-Dahl.* 13 (1936) 53. — *Amyema jambosae* (G.M. Schulze) Danser, *Bull. Jard. Bot. Buitenzorg* III, 14 (1936) 91. — Type: *Peckel* 1222, New Ireland.

Glabrous. *Leaves* opposite; lamina elliptic to ovate, 4–8 by 2–4.5 cm, thin, cuneate at the base to a petiole 10–15 mm long, undulate at the margin, usually acute at the apex, dull on both sides; venation pinnate with the midrib distinct and raised below. *Inflorescences* at the nodes, pedunculate 4- to 7-rayed umbels of triads with the central flowers sessile; peduncle 5–12 mm long; rays 5–8 mm long; pedicels of the lateral flowers 2–3 mm long. *Corolla* in mature bud 5-merous, 14–20 mm long, slender, clavate and obtuse at the apex, mostly red below and yellow or green above. *Anther* 0.7–1.5 mm long, about one quarter as long as the free part of the filament.

Distribution — New Britain, New Ireland.

Habitat & Ecology — Probably in mesic forests, at 0–1060 m altitude; no hosts recorded.

Note — Similar to *Amyema artensis*; for discussion see Barlow, *Blumea* 36 (1992) 351.

37. *Amyema pachypus* (Burkill) Danser

Amyema pachypus (Burkill) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 297; Barlow, Austral. J. Bot. 22 (1974) 582; in Handb. Fl. Papua New Guinea 2 (1981) 218; Van Royen, Alpine Fl. New Guinea 3 (1982) 2262; Barlow, Blumea 36 (1992) 352. — *Loranthus pachypus* Burkill, Kew Bull. (1899) 109. — Type: *Giulianetti s.n.*, Papua New Guinea, Mt Scratchley.

Amyema clavipes Danser, Brittonia 2 (1936) 131; Barlow, Austral. J. Bot. 22 (1974) 570; in Handb. Fl. Papua New Guinea 2 (1981) 211. — Type: *Brass 4972*, Papua New Guinea, Mt Tafa.

Glabrous except for the inflorescence and flowers rarely sparsely brown tomentose, sometimes glaucous. *Leaves* opposite; lamina elliptic to ovate or obovate, mostly 2.5–6 cm long, mostly 1.2–3 cm wide, attenuate to shortly cuneate at the base to a petiole 2–8 mm long, obtuse or rounded at the apex, sometimes with a small mucro, slightly lustrous above, dull below; venation pinnate with the midrib and the main laterals faintly visible. *Inflorescences* at the nodes, pedunculate 3- to 5-rayed umbels of triads with the central flowers sessile; peduncle mostly 8–16 mm long; rays 3.5–7 mm long, usually thicker than the peduncle; pedicels of the lateral flowers 2–4 mm long. *Corolla* in mature bud 4-merous, 14–19 mm long, slender, clavate and rounded at the apex, pink to dark red. *Anther* 0.5–1 mm long, about one third as long as the free part of the filament.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Subalpine communities, from 2300 to 3800 m altitude; recorded hosts include *Dacrycarpus*, *Drimys*, *Podocarpus*, *Prunus*, *Rapanea*, and *Rhododendron*. Hosts other than dicotyledons are rare in *Loranthaceae*.

38. *Amyema plicatula* (K. Krause) Danser

Amyema plicatula (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 298; 11 (1931) 342; Barlow, Blumea 36 (1992) 353. — *Loranthus plicatulus* K. Krause, Nova Guinea 14 (1923) 102. — Type: *Lam 641*, New Guinea, Irian Jaya, 'Pionierbivak'.

Amyema obovata Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 340; Barlow in Handb. Fl. Papua New Guinea 2 (1981) 217. — Type: *Lam 591*, Irian Jaya, 'Pionierbivak'.

Amyema ovariola Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 340. — Type: *Docters van Leeuwen 9383*, Irian Jaya, 'Pionierbivak'.

Amyema cephalanthera Danser, Brittonia 2 (1936) 131. — Type: *Brass 6023*, Papua New Guinea, Oriomo River.

Amyema pentactis Danser, Blumea 3 (1940) 397; Barlow in Handb. Fl. Papua New Guinea 2 (1981) 218. — Type: *Clemens 8307a*, Papua New Guinea, 'Sattelberg'.

Amyema duurenii Barlow, Proc. Roy. Soc. Queensl. 75 (1964) 13. — Type: *van Duuren s.n.*, Papua New Guinea, Kairuku.

Amyema angularis Barlow, Austral. J. Bot. 22 (1974) 565; in Handb. Fl. Papua New Guinea 2 (1981) 208. — Type: *Eyma 5387*, Irian Jaya, Wissel Lake region.

Glabrous except for the inflorescence and flowers rarely sparsely brown- or white-tomentose. *Leaves* opposite, ternate, scattered ternate or rarely quaternate; lamina elliptic to ovate or obovate or rarely almost orbicular, mostly 7–13 cm long, mostly 5–8 cm wide, attenuate or cuneate at the base to a petiole mostly 5–15 mm long, broadly acute to rounded at the apex, dull on both sides; venation pinnate with the midrib raised below and other venation obscure. *Inflorescences* at the nodes, pedunculate 4- to 8-rayed umbels of triads with all flowers sessile; peduncle mostly 12–25 mm long; rays 4–10 mm

long. *Corolla* in mature bud 5- or 6-merous, 16–28 mm long, slender, obtuse or rounded at the apex, pink or red. *Anther* c. 2 mm long, about one quarter as long as the free part of the filament. — **Fig. 8e.**

Distribution — Eastern Australia; *Malesia*: New Guinea, New Britain.

Habitat & Ecology — Primary and secondary humid forests, mostly 0–500 m altitude, rarely to 2400 m; recorded hosts include *Calophyllum*, *Discocalyx*, *Dysoxylum*, *Galbulimima*, *Maniltoa*, and *Pasania*.

Note — Closely related to *Amyema scandens*; for differences and species circumscription see Barlow, *Blumea* 36 (1992) 353.

39. *Amyema polillensis* (C.B. Rob.) Danser

Amyema polillensis (C.B. Rob.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 298. — *Loranthus polillensis* C.B. Rob., Philipp. J. Sc., Bot. 6 (1911) 200. — Type: *McGregor BS 10384*, lecto, Philippines, Polillo.

Glabrous. *Leaves* verticillate in whorls of 4–7; lamina elliptic, c. 17 cm long, c. 7 cm wide, attenuate at the base to a petiole 15–25 mm long, shortly acuminate and acute at the apex, thick, dull on both sides; venation pinnate with the midrib visible above and raised below. *Inflorescences* at the nodes, pedunculate 4- to 6-rayed simple umbels; peduncle 8–11 mm long, dilated at the apex; pedicels c. 4 mm long. *Corolla* in mature bud 4-merous, 21–23 mm long. *Anther* c. 2.5 mm long, about 3 times as long as the free part of the filament, with a broad flat connective continuous with a flattened filament c. 0.6 mm wide.

Distribution — *Malesia*: Philippines (Luzon, Polillo).

Habitat & Ecology — Probably low altitudes; no hosts recorded.

Note — For discussion of relationships see Barlow, *Blumea* 36 (1992) 355.

40. *Amyema polytrias* Danser

Amyema polytrias Danser, *Blumea* 3 (1940) 391. — Type: *Grevenstuk 212*, Sumba.

Glabrous except for the inflorescence (especially the rays) and the ovary usually with an indumentum of sparse to dense short stiff erect brown or buff hairs. *Leaves* verticillate in whorls of 3–6 or sometimes more; lamina narrowly ovate to ovate, mostly 10–25 cm long, mostly 4–8 cm wide, cuneate at the base to a petiole mostly 10–35 mm long, shortly acuminate and acute at the apex, lustrous olive above, dull brown below; venation pinnate with the midrib and the main laterals faintly visible on both sides. *Inflorescences* at the nodes and along the epicortical runners, pedunculate 9- to 12-rayed umbels of triads with all flowers pedicellate; peduncle 10–30 mm long, globose at the apex with a deflexed lip; rays mostly 3.5–5.5 mm long; pedicels variable, 0.2–3 mm long. *Corolla* in mature bud 4-merous, 25–40 mm long, slender, weakly clavate and acute at the apex, pink or red below and yellow or green above. *Anther* 2–3.5 mm long, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Celebes, Sumba, Moluccas.

Habitat & Ecology — 0–2200 m altitude; the only recorded host is *Knema*.

Note — For discussion of species distinction in the *Amyema polytrias* complex, and relationships, see Barlow, Blumea 36 (1992) 356.

41. *Amyema queenslandica* (Blakely) Danser

Amyema queenslandica (Blakely) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 298; Barlow, Blumea 36 (1992) 359. — *Loranthus queenslandicus* Blakely, Proc. Linn. Soc. New S Wales 47 (1922) 392. — Type: *Dixon s.n.*, Queensland, near Herberton.

Amyema involvens Barlow, Austral. J. Bot. 22 (1974) 578; in Handb. Fl. Papua New Guinea 2 (1981) 216. — Type: *Barlow 943*, Papua New Guinea, Mt Kaindi.

Glabrous except for the young shoots, inflorescences and sometimes the flowers sparsely tomentose. *Leaves* opposite; lamina ovate to orbicular or broadly spatulate, 3–8 by 2.5–6 cm, shortly cuneate at the base to a petiole 5–10 mm long, thick, rounded at the apex, slightly lustrous above, dull below; venation almost curvinerved, indistinct. *Inflorescences* at the nodes, pedunculate 4- to 8-rayed robust umbels of triads with the central flowers sessile; peduncle 10–25 mm long; rays 5–10 mm long; pedicels of the lateral flowers 3–5 mm long; bracts dimorphic, the central ones acute, erect, the lateral ones concave, rounded, enclosing the ovary. *Corolla* in mature bud 5- or 6-merous, 30–35 mm long, robust, obtuse at the apex, mostly yellow, rarely orange or red. *Anther* 3–4 mm long, about equal to the free part of the filament.

Distribution — Australia (North Queensland); *Malesia*: New Guinea.

Habitat & Ecology — Humid forests, 840–2440 m altitude in New Guinea; recorded hosts there include *Nothofagus* and *Timonius*.

42. *Amyema rhytidoderma* Barlow

Amyema rhytidoderma Barlow, Blumea 36 (1992) 359. — Type: *Jacobs 7332*, Luzon, Mt Pulog.

Glabrous except for inflorescences and flowers with a dense indumentum of short, straight or crisped, white to brown, simple hairs. *Leaves* quaternate; lamina ovate, 7.5–10 by 3.5–5.5 cm, contracted to truncate at the base, sessile or with a petiole to 2 mm long, acute at the apex, olive green and finely rugose above, pale brown and smooth below; venation pinnate, visible on both surfaces with the midrib raised below. *Inflorescences* at the nodes, pedunculate 3-rayed umbels of triads with all flowers pedicellate; peduncle c. 4 mm long; rays c. 1 mm long; pedicels 0.5–1 mm long. *Corolla* in bud (perhaps immature) 4-merous, c. 18 mm long, slender, acute, bright red. *Anther* c. 2 mm long, about equal to the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — 2300–2500 m altitude; no host recorded.

Note — Closely related to *Amyema luzonensis* and *A. benguetensis*; for differences and species circumscription see Barlow, Blumea 36 (1992) 314.



Fig. 7. *Amyema rigidiflora* (K. Krause) Danser. Kubor Range, Papua New Guinea (Vink 16386). Photo W. Vink, 1963.

43. *Amyema rigidiflora* (K. Krause) Danser

Amyema rigidiflora (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 298; Barlow, Blumea 36 (1992) 360. — *Loranthus rigidiflorus* K. Krause, Bot. Jahrb. 57 (1922) 465. — *Amyema strongylophylla* subsp. *rigidiflora* (K. Krause) Barlow, Austral. J. Bot. 22 (1974) 594; in Handb. Fl. Papua New Guinea 2 (1981) 224. — Type: *Ledermann 9095*, lecto, New Guinea, Sepik.
Loranthus obtusus K. Krause, Bot. Jahrb. 57 (1922) 479, 480. — Type: *Schlechter 17991*, Papua New Guinea, Finisterre Mts.
Loranthus barbellatus Blakely, Proc. Roy. Soc. Queensl. 34 (1922) 27. — *Amyema barbellata* (Blakely) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 294; 11 (1931) 324. — *Amyema strongylophylla* subsp. *barbellata* (Blakely) Barlow, Austral. J. Bot. 22 (1974) 594; in Handb. Fl. Papua New Guinea 2 (1981) 224. — Type: *White 231*, Papua New Guinea, Finisterre Mts.

Glabrous except for the inflorescence and usually the flowers sparsely to densely brown or yellow-brown tomentose. *Leaves* opposite; lamina broadly obovate to nearly orbicular, mostly 4–10 cm long, mostly 3.5–6 cm wide, shortly cuneate at the base to a petiole 5–10 mm long, rounded at the apex, dull on both sides; venation pinnate but somewhat curvinerved with the midrib and the main laterals visible on both sides. *Inflorescences* at the nodes, pedunculate 7- to 12-rayed umbels of triads with the central flowers sessile; peduncle 15–30 mm long, robust, dilated at the apex; rays 6–13 mm long; pedicels of the lateral flowers 2–4 mm long. *Corolla* in mature bud 5- or 6-merous, 20–40 mm long, moderately robust, acute to truncate at the apex, mostly orange to red below and often grading to yellow above. *Anther* 3–5 mm long, about equal to the free part of the filament. — **Fig. 3d, 7.**

Distribution — *Malesia*: Celebes (Talaud), New Guinea.

Habitat & Ecology — Open and humid forests, 0–2150 m altitude; recorded hosts include *Aglaia*, *Castanopsis*, *Eucalyptus*, *Macaranga*, and *Saurauia*.

Note — For distinction as a species from *Amyema strongylophylla*, see Barlow, Blumea 36 (1992) 361.

44. *Amyema scandens* (Tiegh.) Danser

Amyema scandens (Tiegh.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 299; Barlow in Handb. Fl. Papua New Guinea 2 (1981) 218. — *Neophylum scandens* Tiegh., Bull. Soc. Bot. France 41 (1894) 509. — Type: *Balansa 498*, New Caledonia, Prony Bay.
 [For a guide to extensive additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 583; Blumea 36 (1992) 362].

Glabrous except for the inflorescence and flowers very rarely shortly and sparsely tomentose. *Leaves* mostly in whorls of 5–8; lamina variable, lanceolate to ovate or rarely broadly ovate or obovate, 5–20 by 2.5–7 cm, attenuate, cuneate or rarely truncate at the base to a petiole 3–15 mm long, mostly acute or obtuse or less often rounded at the apex, dull on both sides or with the upper surface somewhat glossy; venation pinnate with the midrib raised below, otherwise obscure. *Inflorescences* at the nodes and along the epicortical runners, pedunculate 4- to 8-rayed umbels of triads with all flowers sessile; peduncle mostly 6–12 mm long; rays 3–10 mm long. *Corolla* in mature bud 5-



Fig. 8. *Amyema scandens* (Tiegh.) Danser. a. Twig with leaves; b. stem with inflorescences. — *A. friesiana* (K. Schum.) Danser. c. Inflorescence with young fruits; d. triad of flowers. — *A. plicatula* (K. Krause) Danser. e. Inflorescence (a, b: Mayr 640; c: Docters van Leeuwen 11071; d: Ledermann 7019; e: Schlechter 20304). Redrawn from Danser (1931). Scale bars represent 1 cm.

6-merous, 20–40 mm long, slender, acute or shortly rounded at apex, various shades of red. Anther 2.5–4 mm long, about one third as long as the free part of the filament. — **Fig. 8a, b.**

Distribution — New Caledonia; *Malesia*: New Guinea.

Habitat & Ecology — Primary and secondary closed and open humid forests, 0–1600 m altitude; recorded hosts include *Calophyllum*, *Eugenia*, *Garcinia*, *Nothofagus*, and *Terminalia*.

Note — For discussion of species distinction within the *Amyema scandens* complex, see Barlow, *Blumea* 36 (1992) 333, 363, 371.

45. *Amyema scheffleroides* Barlow

Amyema scheffleroides Barlow, *Blumea* 36 (1992) 364. — Type: *Kostermans 18294*, Sumbawa, Mt Batulante.

Glabrous. *Leaves* in whorls of 4–6; lamina ovate, c. 14 cm long, c. 6 cm wide, shortly cuneate at the base to a petiole 15–20 mm long, shortly attenuate and acute at the apex, slightly lustrous above, dull below; venation pinnate with the midrib prominent below, otherwise obscure. *Inflorescences* at the nodes and probably along the epicortical runners, pedunculate c. 6-rayed umbels of triads with all flowers pedicellate; peduncle 3–4 mm long; rays 1.5–2 mm long; pedicels c. 1 mm long or sometimes those of the central flowers shorter. *Corolla* in mature bud 4-merous, c. 33 mm long, inflated in the middle, contracted near the apex and acute, brownish below and dirty yellow grading to green above. *Anther* c. 3 mm long, about twice as long as the free part of the filament.

Distribution — Sumbawa, only known from the type specimen.

Habitat & Ecology — 700–800 m altitude; no host recorded.

Note — Closely related to *Amyema polytrias*; for differences see Barlow, *Blumea* 36 (1992) 364.

46. *Amyema seemeniana* (K. Schum.) Danser

Amyema seemeniana (K. Schum.) Danser, *Bull. Jard. Bot. Buitenzorg* III, 10 (1929) 299; Barlow, *Austral. J. Bot.* 22 (1974) 589; in *Handb. Fl. Papua New Guinea* 2 (1981) 220; *Blumea* 36 (1992) 365. — *Loranthus seemenianus* K. Schum. in K. Schum. & Hollr., *Fl. Kaiser Wilhelm Land* (1889) 106. — Type: *Hollrung 345*, lecto, New Guinea, 'Hatzfeldhafen'.

Glabrous except for the inflorescence and flowers sometimes sparsely to densely brown- or white-tomentose. *Leaves* opposite; lamina broadly lanceolate to broadly ovate, 6–30 by 3–13 cm, shortly cuneate at the base to a petiole 5–18 mm long, obtuse to acuminate and acute at the apex, dull on both sides; venation curvinerved with 3–5 veins distinct on both sides. *Inflorescences* at the nodes, a 2-flowered simple umbel; peduncle 3–8 mm long; pedicels 2–6 mm long. *Corolla* in mature bud usually 5-merous, 30–65 mm long, thin, curved, more or less inflated, acute or obtuse or rounded at the apex, variable in colour but mostly pink or red and often grading to green or yellow above. *Anther* 5–7 mm long, about equal to the free part of the filament. — **Fig. 9a–d.**

Distribution — Australia (Cape York Peninsula); *Malesia*: New Guinea.

Habitat & Ecology — See under the subspecies.

Notes — 1. Closely related to *Amyema squarrosa*; for differences see Barlow, *Blumea* 36 (1992) 365.

2. There are three subspecies which differ in qualitative and quantitative floral characters and in leaf size, and have strong geographic and altitudinal separation; for discussion see Barlow, *Austral. J. Bot.* 22 (1974) 590.

KEY TO THE SUBSPECIES

- 1a. Anthers strongly curved or hooked; the calyx limb short, irregular, usually infolded; leaf lamina to 12 cm long, mostly acuminate and acute **b. subsp. *flexuosa***

- b. Anthers slightly curved or straight; the calyx limb more than 1 mm long, membranous 2
- 2a. Leaf lamina to 10 cm long, not acuminate; corolla 30–35 mm long; ovary constricted below the spreading calyx limb **a. subsp. *seemeniana***
- b. Leaf lamina to 30 cm long, acuminate; corolla 40–65 mm long; ovary not constricted below the erect calyx limb **c. subsp. *melastomatifolia***



Fig. 9. *Amyema seemeniana* (K. Schum.) Danser subsp. *seemeniana*. a. Flower-bearing twig; b. flower bud; c. flower; d. twig with fruits. — *A. fasciculata* (Blume) Danser. e. Twig with flowers; f. inflorescence with young fruits. — *A. beccarii* (Tiegh.) Danser. g. Inflorescence with flower buds; h. flower (a–c: *Hollrung* 345; d: *Schlechter* 18380; e: *Ramos* BS 33296; f: *Bakhuizen van den Brink* 5795; g: *Endert* 1507; h: *Endert* 1882). a–d, f–h Redrawn from Danser (1931); e redrawn from Danser (1935). Scale bars represent 1 cm.

a. subsp. *seemeniana*

Loranthus articulatus K. Krause, Bot. Jahrb. 57 (1922) 485. — *Amyema articulata* (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 293; 11 (1931) 322. — Type: *Schlechter 18380*, Papua New Guinea, Keneyia R.

Distribution — *Malesia*: Northeastern New Guinea.

Habitat & Ecology — Humid forests and disturbed sites, 0–1100 m altitude; recorded hosts include *Acalypha*, *Albizia*, *Ilex*, *Sarcocephalus*, and *Zanthoxylum*.

b. subsp. *flexuosa* Barlow

Amyema seemeniana (K. Schum.) Danser subsp. *flexuosa* Barlow, Austral. J. Bot. 22 (1974) 591. — Type: *Darbyshire 743*, Papua New Guinea, Yule I.

Distribution — Australia (Cape York Peninsula); *Malesia*: New Guinea.

Habitat & Ecology — Humid forests and disturbed sites, 0–480 m altitude; recorded hosts include *Ficus* and *Planchonella*.

c. subsp. *melastomatifolia* (K. Krause) Barlow

Amyema seemeniana (K. Schum.) Danser subsp. *melastomatifolia* (K. Krause) Barlow, Austral. J. Bot. 22 (1974) 591. — *Loranthus melastomatifolius* K. Krause, Bot. Jahrb. 57 (1922) 465, 488. — Type: *Schlechter 17809*, Papua New Guinea, Kani Mts.

Distribution — *Malesia*: Northeastern New Guinea.

Habitat & Ecology — Humid forests, 1000–2150 m altitude; recorded hosts include *Nauclea* and *Psychotria*.

Note — The original spelling of the epithet is followed here; Danser in Bull. Jard. Bot. Buitenzorg III, 10 (1929) 297 amended it to *melastomifolia*, and was followed by Barlow in Austral. J. Bot. 22 (1974) 591 and Blumea 36 (1992) 365.

47. *Amyema seriata* (Merr.) Barlow

Amyema seriata (Merr.) Barlow, Blumea 36 (1992) 365. — *Loranthus seriatus* Merr., Philipp. J. Sc., Bot. 9 (1914) 285. — *Dicymanthes seriata* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 311. — Type: *Reillo BS 16424*, lecto, Mindanao, Mt Pulongbato.

Glabrous. *Leaves* opposite; lamina ovate, 8–16 by 4.5–7.5 cm, cuneate to rounded at the base to a petiole 5–8 mm long, shortly acuminate and broadly acute at the apex, dull on both sides but darker above; venation pinnate with the midrib and the incurved main laterals prominent on both sides and the midrib raised below. *Inflorescences* at the nodes and along the internodes and epicortical runners, a 6-flowered head of 2 sessile triads on a peduncle 2–4 mm long. *Corolla* in mature bud 5-merous, c. 17 mm long, weakly inflated at the base, clavate and acute at the apex. *Anther* 2.5–4 mm long, sessile or nearly so.

Distribution — *Malesia*: Philippines (Mindanao).

Habitat & Ecology — Possibly in highlands; no hosts recorded.

Notes — 1. Similar to *Amyema hexantha*; for differences see Barlow, *Blumea* 36 (1992) 366.

2. For discussion of equivalence of *Dicymanthes* and *Amyema*, see Barlow, *Blumea* 36 (1992) 298.

48. *Amyema squarrosa* (K. Krause) Danser

Amyema squarrosa (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 299; Barlow, Austral. J. Bot. 22 (1974) 591; in Handb. Fl. Papua New Guinea 2 (1981) 222; *Blumea* 36 (1992) 366. — *Loranthus squarrosus* K. Krause, Bot. Jahrb. 57 (1922) 485. — Type: *Ledermann 10377*, lecto, Papua New Guinea, 'Lordberg'.

Glabrous except for the inflorescence and flowers sometimes sparsely brown-tomentose. *Leaves* opposite; lamina lanceolate to broadly ovate, 8–18 by 2.5–6 cm, shortly cuneate at the base to a petiole 4–9 mm long, acuminate and acute at the apex, dull on both sides; venation pinnate but somewhat curvinerved with the veins distinct below. *Inflorescences* at the nodes, a 2-flowered simple umbel; peduncle obscure or up to 1 mm long; pedicels 2–4 mm long. *Corolla* in mature bud 5-merous, 25–36 mm long, thin, more or less inflated, acute or obtuse or rounded at the apex, variable in colour but mostly pink or red and often grading to green or yellow above. *Anther* 2.5–3 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Probably in closed humid forests, mostly from 1000 to 1100 m altitude, rarely in lowlands; the only recorded host is *Saurauia*.

Note — Closely related to *Amyema seemeniana*; for differences see Barlow, *Blumea* 36 (1992) 365.

49. *Amyema strongylophylla* (Lauterb.) Danser

Amyema strongylophylla (Lauterb.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 299; Barlow, Austral. J. Bot. 22 (1974) 593; in Handb. Fl. Papua New Guinea 2 (1981) 223. — *Loranthus strongylophyllus* Lauterb., Nova Guinea 8 (1912) 815. — Type: *Gjellerup 307*, lecto, Irian Jaya.

Glabrous except for the inflorescence and flowers densely red-brown tomentose. *Leaves* opposite; lamina broadly obovate to orbicular, 8–13 by 5.5–11 cm, shortly cuneate at the base to a petiole 5–10 mm long, rounded at the apex, dull on both sides; venation pinnate but somewhat curvinerved with the midrib and the main laterals usually distinct on both sides. *Inflorescences* at the nodes, pedunculate 15- to 20-rayed umbels of triads with the central flowers sessile; peduncle 15–30 mm long, robust, globosely dilated at the apex; rays 6–13 mm long, arising in depressions; pedicels of the lateral flowers 2–4 mm long. *Corolla* in mature bud 5- or 6-merous, c. 50 mm long, acute or obtuse at the apex, mostly red below and sometimes grading to orange above but with the colour partly obscured by the indumentum. *Anther* 5–8 mm long, about equal to the free part of the filament.

Distribution — *Malesia*: Northern New Guinea.

Habitat & Ecology — Lowlands from 0 to 600 m altitude; the only recorded host is *Timonius*.

Note — Additional synonymy given by Barlow, Austral. J. Bot. 22 (1974) 593 is now referred to *Amyema rigidiflora*; for discussion, distinction as a species and differences from *A. rigidiflora*, see Barlow, Blumea 36 (1992) 367.

50. *Amyema tetraflora* (Barlow) Barlow

Amyema tetraflora (Barlow) Barlow, Austral. J. Bot. 22 (1974) 595; in Handb. Fl. Papua New Guinea 2 (1981) 224; Blumea 36 (1992) 369. — *Ungula tetraflora* Barlow, Proc. Roy. Soc. Queensl. 75 (1964) 16. — Type: *van Duuren s.n.*, Papua New Guinea, Ukua.

Glabrous except for the inflorescence and flowers sparsely tomentose. *Leaves* opposite; lamina broadly lanceolate to ovate, 17–25 by 7–12 cm, rounded to slightly cordate at the base to a petiole 2–4 mm long, acuminate and acute at the apex, glossy above, dull below; venation pinnate, distinct, with the main laterals incurved near the margin. *Inflorescences* at the nodes and along the epicortical runners, pedunculate 4- to 6-rayed umbels of tetrads with all flowers sessile; peduncle 2–4 mm long; rays 1–2.5 mm long. *Corolla* in mature bud 6-merous, 26–32 mm long, slender, slightly clavate and obtuse at the apex, light mauve; petals after anthesis coherent in the lower 4–5 mm. *Anther* c. 3 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: Papua New Guinea (Kairuku Subprovince).

Habitat & Ecology — 0–50 m altitude; no hosts recorded.

Note — Similar to *Amyema brassii*; for differences see Barlow, Blumea 36 (1992) 369.

51. *Amyema tetrapetala* (Danser) Barlow

Amyema tetrapetala (Danser) Barlow, Austral. J. Bot. 22 (1974) 595; in Handb. Fl. Papua New Guinea 2 (1981) 225; Blumea 36 (1992) 369. — *Dicymanthes tetrapetala* Danser, Blumea 3 (1940) 399. — Type: *Womersley NGF 19321*, neo, Papua New Guinea, Wagau.

Glabrous except for young parts, inflorescence and ovary shortly brown-tomentose. *Leaves* opposite; lamina broadly lanceolate, mostly 10–15 cm long, 4–8 cm wide, attenuate at the base to a petiole c. 5 mm long, acuminate and acute at the apex, dull on both sides but slightly darker above; venation pinnate with the midrib and the main laterals visible above and raised below. *Inflorescences* at the nodes; a 6-flowered head of 2 sessile triads on a peduncle 3–6 mm long, subtended by 6 bracts c. 6 mm long. *Corolla* in mature bud 4-merous, 35–42 mm long, slender, acute at the apex, angular, red below grading to orange or yellow above. *Anther* 3–4 mm long, about one third as long as the free part of the filament.

Distribution — *Malesia*: Papua New Guinea (Morobe Province).

Habitat & Ecology — Primary humid forests, 1200–2200 m; no hosts recorded.

Note — For discussion of equivalence of *Dicymanthes* and *Amyema*, see Barlow, Blumea 36 (1992) 298, 369.

52. *Amyema triantha* (Korth.) Tiegh.

Amyema triantha (Korth.) Tiegh., Bull. Soc. Bot. France 41 (1894) 507. — *Loranthus trianthus* Korth., Verh. Bat. Genootsch. 17 (1839) 227, 265. — Type: *Korthals s.n.*, Borneo, near Drongo.
[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 350].

Glabrous except for the inflorescence and flowers shortly tomentose when young. *Leaves* opposite; lamina elliptic to obovate, 10–16 by 6–12 cm, cuneate at the base to an obscure petiole c. 5–10 mm long, obtuse or rounded at the apex, dull on both sides; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes, pedunculate c. 6-rayed umbels of triads with all flowers sessile; peduncle 15–18 mm long; rays 5–7 mm long. *Corolla* in mature bud 6-merous, c. 20 mm long, weakly clavate and obtuse at the apex. *Anther* c. 1.5 mm long, about one third or half as long as the free part of the filament.

Distribution — *Malesia*: Borneo.

Habitat & Ecology — Apparently in lowlands; no hosts recorded.

Note — For discussion of species distinction within the *Amyema scandens* complex, see Barlow, Blumea 36 (1992) 333, 363, 371.

53. *Amyema tristis* (Zoll.) Tiegh.

Amyema tristis (Zoll.) Tiegh., Bull. Soc. Bot. France 41 (1894) 507; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 351; Backer & Bakh. f., Fl. Java 2 (1965) 71; Barlow, Blumea 36 (1992) 371. — *Loranthus tristis* Zoll., Nat. Geneesk. Arch. 2 (1845) 579. — *Phoenicanthemum triste* (Zoll.) Miq., Fl. Ind. Bat. 1, 1 (1856) 826. — Type: *Zollinger 2937*, Java, Mt Raung.
Dicymanthes elliptica Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 364. — Type: *Iboet 509*, Sumba, Kananggar.

Glabrous except for the flowers sometimes sparsely hairy. *Leaves* opposite; lamina elliptic to ovate or rarely obovate, 6–15 by 3–7.5 cm, cuneate at the base, sessile or with a short petiole to 3 mm long, somewhat acuminate and obtuse to acute at the apex, dull on both sides; venation pinnate with the midrib and the main laterals visible. *Inflorescences* at the nodes, pedunculate subcapitate usually 2-rayed umbels of triads with all flowers sessile; peduncle 1.5–5 mm long; rays mostly 1–2 mm long (but rarely obscure, with inflorescence then a 6-flowered head of 2 sessile triads). *Corolla* in mature bud 5-merous, 14–21 mm long, weakly clavate and obtuse at the apex, mostly red, sometimes golden below. *Anther* 2–3 mm long, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Java, Lesser Sunda Islands (Bali, Sumba, Flores).

Habitat & Ecology — 575–1500 m altitude; recorded hosts include *Bischofia* and *Villebrunea*.

Note — For discussion of equivalence of *Dicymanthes* and *Amyema*, see Barlow, Blumea 36 (1992) 298, 372.

54. *Amyema umbellata* Danser

Amyema umbellata Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 352. — Type: *Toxopeus 215*, Moluccas, Buru.

Glabrous except for the inflorescence and ovary papillose hairy. *Leaves* opposite, ternate or quaternate; lamina lanceolate, 10–16 by 2.5–4.5 cm, cuneate at the base to a petiole 10–15 mm long, acuminate and acute at the apex, dull on both sides; venation pinnate with the midrib and the main laterals distinct. *Inflorescences* at the nodes, pedunculate c. 12-rayed simple umbels; peduncle 4–5 mm long; pedicels c. 2.5 mm long. *Corolla* in mature bud 5-merous, 30–32 mm long, broadly acute at the apex, light pink. *Anther* c. 3 mm long, about equal to the free part of the filament.

Distribution — *Malesia*: Moluccas (Buru).

Habitat & Ecology — No host recorded.

Note — A doubtful species, possibly rare; see also Barlow, *Blumea* 36 (1992) 373.

55. *Amyema urdanetensis* (Elmer) Danser

Amyema urdanetensis (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 299. — *Loranthus urdanetensis* Elmer, Leaflet Philipp. Bot. 6 (1913) 1963. — Type: *Elmer 14092*, lecto, Mindanao, Mt Urdaneta. [For additional synonymy see Danser, Philipp. J. Sc. 58 (1935) 68].

Glabrous except for the inflorescence and ovary densely tomentose. *Leaves* opposite, sometimes scattered; lamina lanceolate, 4–8 by 1–3 cm, cuneate to somewhat rounded at the base to a petiole 5–12 mm long, somewhat acuminate and acute at the apex, more or less glossy and darker above, dull below; venation pinnate with the midrib raised below and visible above and the main laterals indistinct. *Inflorescences* at the nodes, pedunculate 5- to 8-rayed umbels of triads with the central flowers sessile; peduncle 20–30 mm long; rays 2–5 mm long; pedicels of the lateral flowers c. 0.5 mm long. *Corolla* in mature bud 5-merous, 30–35 mm long, slightly dilated upwards, weakly clavate and obtuse at the apex, yellow, or red below and yellow above. *Anther* 1.5–2 mm long, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Philippines (Leyte, Mindanao).

Habitat & Ecology — Recorded from 1830 m altitude; no host recorded.

Note — Similar to *Amyema queenslandica* and *A. rigidiflora*; for discussion see Barlow, *Blumea* 36 (1992) 373.

56. *Amyema vernicosa* Barlow

Amyema vernicosa Barlow, *Blumea* 36 (1992) 373. — Type: *Mendoza 1479 (PNH 18467)*, Luzon, Mayon Volcano.

Glabrous except for the inflorescence and flowers sparsely to densely tawny- or brown-tomentose. *Leaves* ternate (sometimes scattered); lamina ovate or lanceolate-ovate, 4–7 by 2.5–3.5 cm, cuneate at the base to a petiole 12–20 mm long, acute or rounded-obtuse at the apex, distinctly shining above, dull below; venation pinnate, obscure above and the midrib raised and the main laterals distinct below. *Inflorescences* at the nodes, pedunculate 3-rayed umbels of triads with all flowers sessile; peduncle 12–15 mm long; rays 0.5–1 (rarely to 3.5) mm long. *Corolla* in mature bud 4- or 5-merous, c. 25 mm long, red below grading to yellow and green above. *Anther* c. 1.5 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — Recorded from 1000 m altitude; no host recorded.

Note — For a discussion of the specific distinction of *Amyema vernicosa*, see Barlow, *Blumea* 36 (1992) 374.

57. *Amyema verticillata* (Merr.) Danser

Amyema verticillata (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 299. — *Cleistoloranthus verticillatus* Merr., Philipp. J. Sc., Bot. 4 (1909) 150. — Type: Curran, Merritt & Zschokke FB 16229, Luzon, Mt Pulog.

[For additional synonymy see Danser, Philipp. J. Sc. 58 (1935) 79].

Glabrous. *Leaves* quaternate; lamina lanceolate-oblong, mostly 3–6 cm long, 1–3 cm wide, cuneate at the base to a petiole 3–10 mm long, shortly acuminate and acute or obtuse at the apex, dull on both sides but darker above; venation pinnate with the midrib raised below and other veins indistinct. *Inflorescences* at the nodes, pedunculate 4-rayed umbels of triads with all flowers pedicellate or the central flower sessile; peduncle 10–15 mm long; rays 5–7 mm long; pedicels of the central flowers very short or obscure; pedicels of the lateral flowers 1–1.5 mm long. *Corolla* in mature bud 4-merous, 13–14 mm long, slender, clavate and truncate at the apex, with a corona formed from spreading, bilobed dorsal appendages up to 1.2 mm long, pink or red, sometimes grading to yellow above. *Anther* 1–1.5 mm long, about one third as long as the free part of the filament.

Distribution — *Malesia*: Philippines (Northern Luzon).

Habitat & Ecology — Highlands, 1670–2500 m altitude; no hosts recorded.

Note — The corona on the corolla is distinctive; for discussion see Barlow, *Blumea* 36 (1992) 374.

58. *Amyema wenzelii* (Merr.) Danser

Amyema wenzelii (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 299. — *Loranthus wenzelii* Merr., Philipp. J. Sc., Bot. 8 (1913) 370. — Type: Wenzel 24, lecto, Leyte.

Glabrous. *Leaves* quaternate; lamina oblong or ovate, 11–27 by 5–15 cm, cuneate to rounded at the base to a petiole 10–20 mm long, acuminate and obtuse at the apex, dull on both sides; venation pinnate with the midrib and the main laterals distinct and the midrib raised below. *Inflorescences* many at the nodes and along the internodes and epicortical runners, apparently sessile mostly 2- or 3-flowered umbels; peduncle rudimentary, immersed in the bark; pedicels up to 2 mm long. *Corolla* in mature bud 5-merous, 12–14 mm long, slightly inflated, obtuse at the apex, yellow below and green above. *Anther* c. 2.5 mm long, sessile, with a broad flat connective continuous with a flattened filament c. 0.5 mm wide decurrent on the face of the petal.

Distribution — *Malesia*: Philippines (Leyte, Bohol).

Habitat & Ecology — 60–800 m altitude; no hosts recorded.

Note — Closely related to *Amyema beccarii*; for distinction as a species see Barlow, *Blumea* 36 (1992) 375.

59. *Amyema wichmannii* (K. Krause) Danser

Amyema wichmannii (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 299; Barlow, Austral. J. Bot. 22 (1974) 596; in Handb. Fl. Papua New Guinea 2 (1981) 225; P. Royen, Alpine Fl. New Guinea 3 (1982) 2266; Barlow, Blumea 36 (1992) 376. — *Loranthus wichmannii* K. Krause, Bot. Jahrb. 57 (1922) 465. — Type: *Pulle* 979, lecto, Irian Jaya, Wichmann Mts.
Loranthus keysseri K. Krause, Bot. Jahrb. 62 (1929) 474. — Type: *Keysser s.n.*, Papua New Guinea, Saruwaged Mts.

Glabrous except for a few cilia on the bracts. *Leaves* opposite; lamina broadly lanceolate to almost orbicular, mostly 4–10 cm long, mostly 2–4 cm wide, cuneate at the base to a petiole 2–8 mm long, usually acute or obtuse with a small mucro at the apex, lustrous above, dull below; venation pinnate, mostly obscure. *Inflorescences* at the nodes, pedunculate 6- to 12-rayed umbels of triads with all flowers pedicellate or the central flowers sessile; peduncle mostly 22–40 mm long, dilated up to 3 mm wide at the apex; rays mostly 6–10 mm long; pedicels of the central flowers 0–4 mm long; pedicels of the lateral flowers 1.5–5 mm long; bracts with rounded dorsal protuberances. *Corolla* in mature bud 4-merous, mostly 20–28 mm long, slender, strongly clavate and acute or rounded at the apex, red, often nearly black in the lower part. *Anther* 1–2 mm long, about equal to or half as long as the free part of the filament.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — See under the subspecies.

Notes — 1. Related to *Amyema dilatipes* and *A. pachypus*; for discussion see Barlow, Blumea 36 (1992) 377.

2. There are two subspecies which differ in inflorescence characters and have geographic separation; for discussion see Barlow, Austral. J. Bot. 22 (1974) 590; Blumea 36 (1992) 377.

KEY TO THE SUBSPECIES

- 1a. Central flower of the triad usually on a pedicel 2–4 mm long with the bract at its base; leaves with pustular spots below a. subsp. **wichmannii**
- b. Central flower of the triad sessile; leaves mostly lacking pustular spots below b. subsp. **purum**

a. subsp. **wichmannii**

Distribution — Irian Jaya, Papua New Guinea (Star Mts).

Habitat & Ecology — Subalpine communities mostly from 2800 to 3420 m altitude, rarely down to 2000 m; recorded hosts include *Drimys*, *Rapanea*, *Rhododendron*, and *Vaccinium*.

b. subsp. **purum** Barlow

Amyema wichmannii (K. Krause) Danser subsp. *purum* Barlow, Austral. J. Bot. 22 (1974) 597. — Type: Brass 30674, Papua New Guinea, Mt Wilhelm.

Distribution — Papua New Guinea.

Habit & Ecology — Subalpine communities from 2350 to 3680 m altitude; recorded hosts include *Ardisia*, *Drimys*, *Eurya*, *Rapanea*, and *Rhododendron*.

AMYLOTHECA

Amylothea Tiegh., Bull. Soc. Bot. France 41 (1895) 261. — Type species: *Amylothea dictyophleba* (F. Muell.) Tiegh.

[For additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 545; in Flora of Australia 22 (1984) 73].

Aerial stem-parasitic shrubs, often robust, with epicortical runners bearing secondary haustoria. *Leaves* mostly opposite, sometimes displaced; venation pinnate. *Inflorescences* axillary, primarily a raceme of decussate pairs of pedunculate dichasia (triads), sometimes variously reduced (see below); bracts single under each flower, not enlarged to form an involucre. *Corolla* 6-merous, regular, gamopetalous. *Anthers* basifixed, immobile. *Style* simple, articulate above the base, usually with a small knob-like stigma. *Fruit* ellipsoid to globular, usually with a persistent nipple-like style base. — **Fig. 10, 11.**

Distribution — Four species distributed from Thailand and Peninsular Malaysia eastwards and southwards to New Guinea, Australia, New Caledonia and New Hebrides. In *Malesia* 3 species, 1 in northwestern Malesia and 2 in New Guinea.

Habitat & Ecology — Humid forests and open woodlands, common in lowlands but extending to montane forests at 2850 m in New Guinea. Host specificity is low.

Morphology — The plesiomorphic inflorescence state for the genus is an axillary raceme of uniformly spaced opposite pairs of triads. Simpler inflorescences are derived by reduction, and occur primarily as infraspecific rather than interspecific variations. The inflorescence is often subumbellate, and the triads may be reduced to single flowers so that the inflorescence may appear to be a simple raceme or even a 2-flowered simple umbel (Fig. 10).

Taxonomy — Danser (1931) included *Decaishnina* in *Amylothea*, which was therefore more broadly circumscribed than it is here. *Amylothea* is closely related to *Decaishnina*, which is probably the least specialized genus in the group. The major difference is in the corolla, which is essentially choripetalous in *Decaishnina*, although usually with the petals coherent at the base into a short tube, and distinctly gamopetalous to the middle or higher in *Amylothea*. For further discussion of generic relationships see Barlow, Blumea 38 (1993) 110.

KEY TO THE SPECIES

- 1a. Leaves more or less glaucous; lamina truncate or shortly cuneate at the base into a sharply defined dark coloured petiole more than 10 mm long; style articulate 0–0.5 mm above the base **3. *A. duthieana***
- b. Leaves not glaucous; lamina attenuate at the base into an obscure winged petiole less than 10 mm long; style articulate 2–3 mm above the base **2**

- 2a. Leaves mostly acuminate and acute at the apex, 12–20 cm long; inflorescence parts robust; peduncles of the triads mostly 1–3 mm long **1. *A. acuminatifolia***
 b. Leaves mostly rounded, rarely acute at the apex, 5–14 cm long; inflorescence parts slender; peduncles of the triads mostly 3–7 mm long **2. *A. dictyophleba***

1. *Amylothea acuminatifolia* Barlow

Amylothea acuminatifolia Barlow, Austral. J. Bot. 22 (1974) 545; in Handb. Fl. Papua New Guinea 2 (1981) 227. — Type: *Eyma* 4888, Irian Jaya, 'Prauwbivak'.

Glabrous. *Leaves* opposite; lamina narrowly ovate, 12–20 by 2.5–7 cm, attenuate at the base to an obscure winged petiole 2–5 mm long, acuminate and acute at the apex, lustrous above, dull below; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes, a raceme of 2 or 3 decussate pairs of triads with the central flowers sessile and the lateral flowers pedicellate; axis 6–10 mm long; peduncles of the triads 1–3(–6) mm long; pedicels of the lateral flowers 2–5 mm long. *Corolla* in mature bud 6-merous, 45–65 mm long, robust, slightly inflated, weakly clavate and acute or obtuse at the apex, red below and yellow above; tube in the open flower 25–35 mm long. *Anther* 5–7 mm long, acute, about equal to the free part of the filament. *Style* articulate 2–3 mm above the base.

Distribution — *Malesia*: New Guinea (Irian Jaya).

Habitat & Ecology — Probably in closed humid forests from 1650 to 2850 m altitude; no hosts recorded.

Note — For differences from *Amylothea dictyophleba* see Barlow, *Blumea* 38 (1993) 111.

2. *Amylothea dictyophleba* (F. Muell.) Tiegh.

Amylothea dictyophleba (F. Muell.) Tiegh., Bull. Soc. Bot. France 41 (1894) 262; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1936) 242; Barlow, Austral. J. Bot. 22 (1974) 547; in Handb. Fl. Papua New Guinea 2 (1981) 227. — *Loranthus dictyophlebus* F. Muell., Rept. Burdekin Exped. (1860) 14. — Type: *Beckler s.n.*, lecto, New South Wales, Hastings River.
 [For guide to extensive additional synonymy see Barlow, *Blumea* 38 (1993) 111].

Glabrous. *Leaves* opposite; lamina narrowly to broadly ovate or elliptic, 5–14 by 1.5–12 cm, shortly cuneate to truncate at the base to an obscure winged petiole 2–8 mm long, obtuse or rounded or rarely acute at the apex, usually lustrous above, dull below; venation pinnate with the midrib, the main laterals and reticulate veins usually distinct on both sides. *Inflorescences* at the nodes, a raceme of 1–6 decussate, often subumbellate pairs of triads or single flowers; triads (when present) with the central flowers sessile and the lateral flowers pedicellate or sometimes sessile; axis 3–12(–28) mm long; peduncles of the triads or single flowers 3–7(–10) mm long; pedicels of the lateral flowers (when present) 2–4 mm long. *Corolla* in mature bud 6-merous, (28–)35–60 mm long, slightly to strongly inflated, weakly clavate and acute or obtuse at the apex, red or orange or yellow below, usually paler and green or yellow above; tube in the open flower (15–)18–30 mm long. *Anther* (3–)5–8 mm long, acute, about equal to the free part of the filament. *Style* articulate 1–3 mm above the base. — **Fig. 10.**

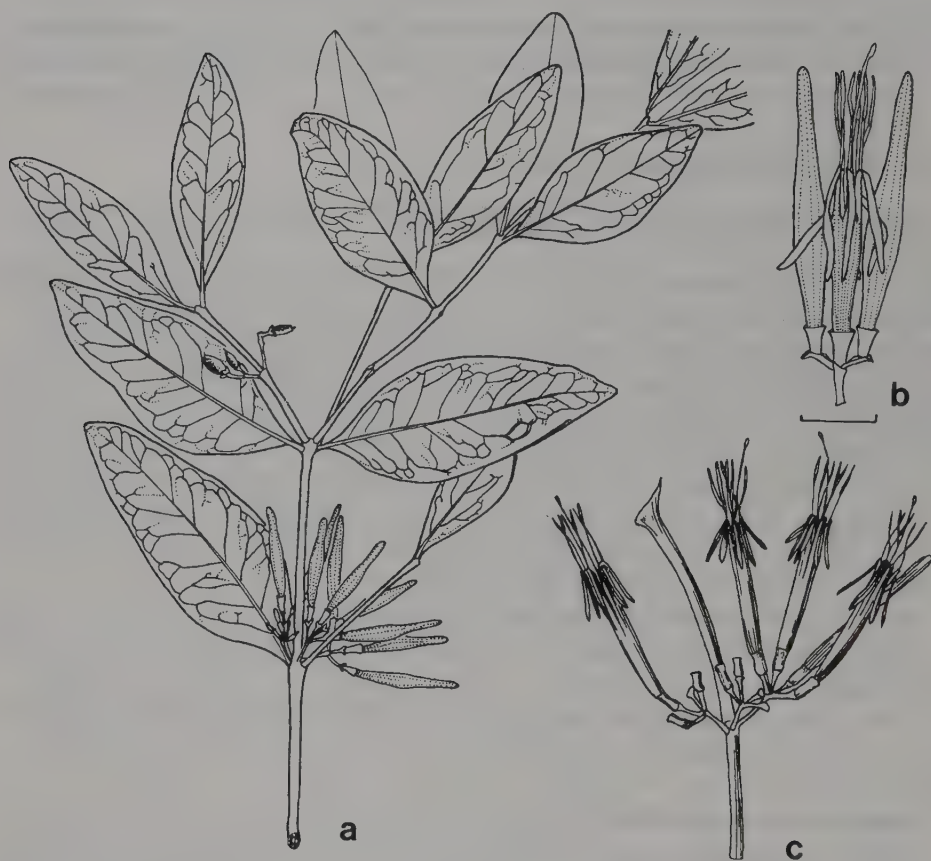


Fig. 10. *Amylothecha dictyophleba* (F. Muell.) Tiegh. a. Flower-bearing twig; b. triad of flowers; c. inflorescence as a few-flowered simple umbel (a, c: not cited; b: *MacKee* 27192). a Redrawn from Barlow (1981); b redrawn from Barlow (1996); c redrawn from Danser (1934). Scale bars represent 1 cm.

Distribution — Eastern Australia, New Caledonia, New Hebrides; *Malesia*: southern New Guinea.

Habitat & Ecology — Mostly in primary and secondary closed forests, 0–1000 m altitude, rarely to 1500 m; recorded on numerous hosts.

Note — For circumscription as a species see Barlow, *Blumea* 38 (1993) 112.

3. *Amylothecha duthieana* (King) Danser

Amylothecha duthieana (King) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 301. — *Loranthus duthieanus* King, J. As. Soc. Beng. 56, ii (1888) 94. — Type: *Scortechini s. n.*, Perak. [For additional synonymy see Barlow, *Blumea* 38 (1993) 112].



Fig. 11. *Amylothecha duthieana* (King) Danser, with spiderhunter (*Arachnothera*), a pollinator bird. Borneo, Sarawak, Lambir Hills Nature Reserve (Nagamasu 4669). Photo Takakazu Yumoto, 1992, with permission.

Glabrous but often glaucous, robust. *Leaves* opposite or scattered; lamina oblong to ovate or broadly elliptic, 7–15 by (2–)3.5–7 cm, thick, truncate or shortly cuneate at the base to a dark-coloured petiole 10–25 mm long, rounded at the apex, dull on both sides; venation pinnate with the midrib and the main laterals distinct on both sides and the midrib prominent and dark-coloured below. *Inflorescences* at the nodes, a raceme of 1–5 decussate pairs of triads with all flowers pedicellate; axis 3–20 mm long; peduncles of the triads 1.5–5 mm long; pedicels of the flowers 0.5–2 mm long. *Corolla* in mature bud 6-merous, 45–70 mm long, robust, gradually widened upwards, weakly clavate and obtuse at the apex, red in the lower part, usually dark purple, brown or black at the apex; tube in the open flower 30–48 mm long. *Anther* 2–3.5 mm long, obtuse, about half as long as the free part of the filament. *Style* articulate c. 0.5 mm above the base. — **Fig. 11.**

Distribution — Peninsular Thailand; *Malesia*: Sumatra, Peninsular Malaysia, Singapore, Borneo.

Habitat & Ecology — Humid forests, 0–700 m altitude; frequently recorded as parasitic on *Shorea*, other recorded hosts include *Dipterocarpus* and *Gonystylus*.

Note — For circumscription as a species see Barlow, *Blumea* 38 (1993) 113.

BARATHRANTHUS

Barathranthus Miq., Fl. Ind. Bat. 1, 1 (1856) 834. — Type species: *Barathranthus axanthus* (Korth.) Miq. [For synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 392].



Fig. 12 & 13. *Barathranthus axanthus* (Korth.) Miq., flower buds (left) & flowers (right). Borneo, W Kalimantan, Pasir Pandjang (Elsener H 98). Photos A. Elsener, 1965.

Aerial stem-parasitic shrubs with epicortical runners bearing secondary haustoria. *Leaves* opposite or displaced, sometimes with fully developed ones alternating with very reduced ones and then sometimes apparently superposed. *Inflorescence* capitate, a very condensed spike, with the flowers placed in small hollows; bracts single under each flower. *Flowers* hermaphrodite or functionally unisexual with plants dioecious. *Corolla* 4-merous, choripetalous, regular. *Anthers* basifixed, immobile. *Style* straight, simple; stigma small. *Fruit* ellipsoid to globose. — **Fig. 12–14.**

Distribution — Four species from Sri Lanka southeastwards to Indochina and Malesia; in *Malesia* 2 species reaching Borneo and Java.

Habitat & Ecology — Probably in humid forests, 0–1900 m altitude. Host specificity is probably low.

Morphology — The flower head is seemingly sessile; its receptacle is the condensed, convex axis of a spike, and the flowers are inserted in small hollows of this axis; the floral bracts enclose the base of each flower but do not form an involucre around the inflorescence.

Taxonomy — The genus is probably related to *Loranthus* and to the larger genus *Helixanthera*, differing in its condensed, capitate inflorescence. It also shares with *Loranthus* the existence of dioecy among its species.

There has been some uncertainty about the spelling of *Barathranthus*. The name was first used by Korthals in Verh. Bat. Genootsch. 17 (1839) 250, 262, as a section of *Loranthus*. Miquel in Fl. Ind. Bat. 1, 1 (1856) 834 raised the section to generic rank, as *Baratranthus*, citing p. 262 of Korthals' work. However, on p. 262 Korthals had used the spelling *Barathranthus*. Miquel's spelling was adopted by Pfeiffer in Index Nom. Gen. (1979) 177, with *Barathranthus* listed as an orthographic variant. In Korthals' original work the orthographically correct *Barathranthus* was used in his enumeration (p. 262), and *Baratranthus* was used in a preamble in Dutch on p. 250 (C. Kalkman, personal communication). The latter spelling is best treated as a typographic error, and *Barathranthus* is accordingly confirmed as the correct spelling.

KEY TO THE SPECIES

- 1a. Young internodes terete; many of the leaves vestigial and deciduous; flowers unisexual, dioecious; corolla less than 8 mm long **1. *B. axanthus***
- b. Young internodes 4-angular; leaves all fully developed; flowers hermaphrodite; corolla more than 10 mm long **2. *B. productus***

1. *Barathranthus axanthus* (Korth.) Miq.

Barathranthus axanthus (Korth.) Miq., Fl. Ind. Bat. 1, 1 (1856) 834; Backer & Bakh. f., Fl. Java 2 (1965) 72. — *Loranthus axanthus* Korth., Verh. Bat. Genootsch. 17 (1839) 262. — Type: *Korthals s.n.*, Sumatra, Mt Malintang.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 393].

Glabrous except for a dense rusty stellate tomentum on the young vegetative parts and inflorescences. Stem internodes somewhat angular when young but soon terete. *Leaves* opposite or displaced, with pairs of normally developed leaves usually separated by one or more pairs of vestigial ones; normally developed lamina narrowly ovate to ovate, 6–16 by 2–7.5 cm, cuneate to truncate at the base to a petiole 5–17 mm long, acuminate and acute at the apex, dull on both sides; venation pinnate with the midrib visible above and prominent below and other venation obscure; vestigial leaves 5–7 mm long, channeled above, deciduous. *Inflorescences* at the nodes, a 6- to 12-flowered capitate spike; axis 1–2 mm long; bracts c. 0.5 mm long, concave. *Flowers* unisexual, dioecious. *Corolla* in mature bud cylindric or somewhat narrowed in the middle, angular, obtuse, in male flowers c. 4 mm long, in female flowers 2.5–3 mm long, usually white to yellow but sometimes pink or red. *Anther* c. 1.5 mm long, not transversely septate, sessile. — **Fig. 12, 13, 14b–d.**

Distribution — Cambodia; *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java.

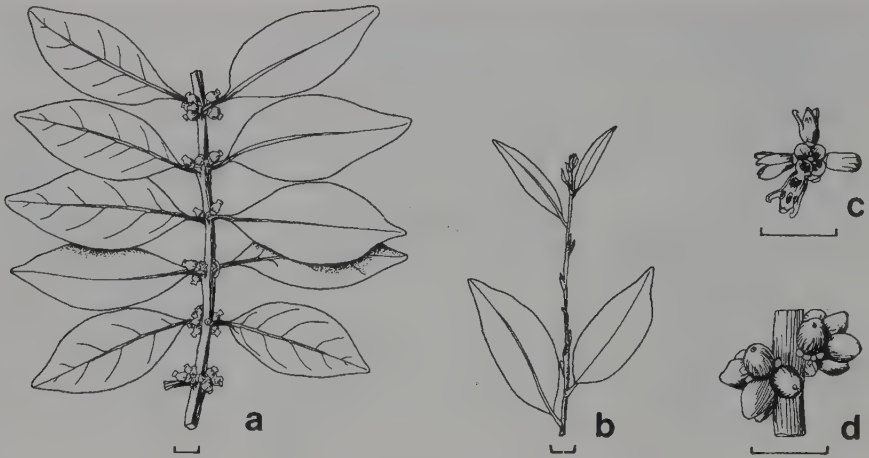


Fig. 14. *Barathranthus productus* (King) Tiegh. a. Fruit-bearing twig. — *B. axanthus* (Korth.) Miq. b. Very young twig with two kinds of leaves; c. male inflorescence from above, with upper four flowers removed; d. portion of stem with two infructescences (a: Wray 2949; b: Sapiin 2610; c: Docters van Leeuwen 7643; d: Docters van Leeuwen 5451). Redrawn from Danser (1931). Scale bars represent 1 cm.

Habitat & Ecology — 0–1900 m altitude; the only recorded hosts are *Antidesma* and *Ficus*.

Note — Apart from probably *Loranthus odoratus*, this is the only dioecious species of *Loranthaceae* in Malesia.

2. *Barathranthus productus* (King) Tiegh.

Barathranthus productus (King) Tiegh., Bull. Soc. Bot. France 41 (1984) 501. — *Loranthus productus* King, J. As. Soc. Beng. 56, ii (1887) 91. — Syntypes: Scortechini 391, 581, Kunstler 3240, Perak. [For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 396].

Glabrous. Stem internodes quadrangular. *Leaves* opposite; lamina narrowly ovate to ovate, 5–13 by 2–6 cm, cuneate at the base to a petiole 6–16 mm long, weakly attenuate and shortly rounded or obtuse at the apex, dull on both sides or darker and slightly lustrous above; venation pinnate with the midrib visible and other veins obscure on both sides. *Inflorescences* at the nodes, a 2- to 6-flowered capitate spike; axis c. 1 mm long; bracts 1.5–2.5 mm long, concave; flowers hermaphrodite. *Corolla* in mature bud 9–13 mm long, cylindric, weakly angular, obtuse or rounded at the apex, white or yellow. *Anther* c. 3 mm long, strongly reflexed, transversely septate, about equal to the free part of the filament. — **Fig. 14a.**

Distribution — *Malesia*: Sumatra, Peninsular Malaysia, Borneo.

Habitat & Ecology — Mostly 900–1800 m altitude; no hosts recorded.



Fig. 15. *Cecarria obtusifolia* (Merr.) Barlow. a. Fruit-bearing twig; b. two-flowered inflorescence; c. twig with four-flowered inflorescence; d. flower in sectional view (a, b, d: not cited; c: Hyland 10884). a, b, d Redrawn from Barlow (1981); c redrawn from Barlow (1984). Scale bars represent 1 cm.

CECARRIA

Cecarria Barlow in Barlow & Wiens, *Brittonia* 25 (1973) 28, 34. — Type species: *Cecarria obtusifolia* (Merr.) Barlow.

Aerial stem-parasitic shrubs (haustorial structure unknown). *Leaves* opposite. *Inflorescences* axillary, a simple 2-flowered umbel, rarely produced into a 4-flowered raceme or spike of decussate pairs; bracts solitary under each flower. *Corolla* 6-merous, chori-petalous, regular. *Stamens* slightly unequal in length; anthers dorsifixed, versatile. *Style* simple, with a knob-like stigma. *Fruit* nearly globular. — **Fig. 15.**

Distribution — Genus of one species ranging from the Philippines to New Guinea, and extending beyond Malesia to Queensland (Cape York Peninsula) and the Solomon Islands.

Habitat & Ecology — Closed and open humid forests, in lowlands and foothills. Host specificity is probably low.

Morphology & Taxonomy — *Cecarria* shows several character states which appear to be primitive for the family, especially its open, pale-coloured, choripetalous, apparently insect-attracting corolla and dorsifixed versatile anthers; for discussion of phylogenetic importance see Barlow in Barlow & Wiens, *Brittonia* 25 (1973) 26; *Blumea* 40 (1995) 16.

Biogeography — The genus *Cecarria* has an unusual distribution which extends across Charles's Line; for discussion see Barlow, *Blumea* 40 (1995) 16.

***Cecarria obtusifolia* (Merr.) Barlow**

Cecarria obtusifolia (Merr.) Barlow in Barlow & Wiens, *Brittonia* 25 (1973) 34; in *Handb. Fl. Papua New Guinea* 2 (1981) 229. — *Phrygilanthus obtusifolius* Merr., *Philipp. J. Sc.* 1, Suppl. (1906) 189. — Type: *Borden FB 1813*, lecto, Luzon, Lamao River.

[For additional synonymy see Barlow, *Austral. J. Bot.* 22 (1974) 557; in *Fl. Austral.* 22 (1984) 90].

Glabrous. *Leaves* opposite; lamina obovate, 3–5.5 by 2–4.5 cm, cuneate at the base to an obscure petiole 2–6 mm long, rounded at the apex, dull on both sides; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* few at the nodes, developing successively, a 2-flowered umbel or produced into a 4-flowered raceme or spike; axis 6–9(–20) mm long; pedicels 0–3 mm long, the lower ones often shorter when the inflorescence is prolonged into a raceme. *Corolla* in mature bud 6-merous, 10–14 mm long, cylindric, weakly clavate and obtuse at the apex, white to pale creamy green; petals reflexed near the middle at anthesis. *Anther* ovoid, c. 1.5 mm long, with a short sterile tip, on a free filament c. 2 mm long. — **Fig. 15.**

Distribution — Solomon Islands, Australia (Cape York Peninsula); *Malesia*: Philippines (Luzon, Mindanao), Lesser Sunda Islands (Flores, Timor), New Guinea.

Habitat & Ecology — Closed and open humid forests, 300–1350 m altitude; recorded hosts include *Calophyllum*, *Casuarina*, *Syzygium*, and *Xanthostemon*.

CYNE

Cyne Danser, *Bull. Jard. Bot. Buitenzorg* III, 10 (1929) 291, 306, — Type species: *Cyne banahaensis* (Elmer) Danser.

[For additional synonymy see Barlow, *Blumea* 38 (1993) 101].

Aerial stem-parasitic shrubs with epicortical runners bearing secondary haustoria. *Leaves* opposite, usually darker and glossier above than below; venation pinnate. *Inflorescences* in the leaf axils or depressions at the stem nodes, developing successively, sessile or almost so, a very contracted or capitate raceme of one or more decussate pairs of dichasia (triads) or rarely dyads, developing beneath the stem periderm which forms

a blister-like calyptra which falls in one piece or ruptures as the flowers expand; triads and individual flowers sessile or with minute peduncles and pedicels, these sometimes developing only in fruit; bracts single under each flower and together forming an involucre under each triad. *Corolla* 6-merous, regular, choripetalous although with the petals coherent into a short tube at the base after anthesis. *Anthers* basifixed, sessile. *Style* simple, often articulate above the base, usually with a small knob-like stigma. *Fruit* ellipsoid, usually with a persistent nipple-like style base. — **Fig. 16.**

Distribution — Six species distributed in eastern *Malesia* from the Philippines to New Guinea.

Habitat & Ecology — Humid and open forests, 0–1500 m altitude; there are no specific host records.

Morphology — The basic inflorescence structure is a raceme of decussate triads, as in *Decaishnina*, but with a very contracted axis. The least specialized inflorescences are very short racemes with only one or two pairs of triads on very short peduncles, whilst the most extreme are sessile heads in depressions in the stem. There is no involucre of imbricate bracts subtending the entire inflorescence, as in some related genera, and the primary diagnostic character for the genus is the bubble-like or pellicle-like calyptra, developed from the stem periderm, which covers the young inflorescence. As the inflorescence expands the calyptra is displaced or irregularly split.

Open flowers of most species are unknown, although the available material suggests that floral characters are relatively uniform.

Taxonomy — The genus is very closely related to *Decaishnina*. Some species show a clear transition to the latter in inflorescence structure, and the diagnostic character for *Cyne* is the presence of the calyptra. For further discussion see Barlow, *Blumea* 38 (1993) 102.

KEY TO THE SPECIES

- 1a. Leaves completely sessile 2
- b. Leaves obscurely to distinctly petiolate 3
- 2a. Leaves of each pair united at the margins into a cup **5. *C. perfoliata***
- b. Leaves of each pair not united at the margins **4. *C. papuana***
- 3a. Inflorescence a sessile head of usually 3 sessile pairs of triads 4
- b. Inflorescence a contracted raceme with an axis 1–4 mm long and usually 1 or 2 pairs of triads 5
- 4a. Young internodes quadrangular; leaves shortly acuminate at the apex **6. *C. quadriangula***
- b. Young internodes terete; leaves obtuse or rounded at the apex **2. *C. banahaensis***
- 5a. Inflorescence axis 3–4 mm long; triads pedunculate; lateral flowers shortly pedicellate **1. *C. baetorta***
- b. Inflorescence axis c. 1 mm long; triads and lateral flowers sessile **3. *C. monotrias***

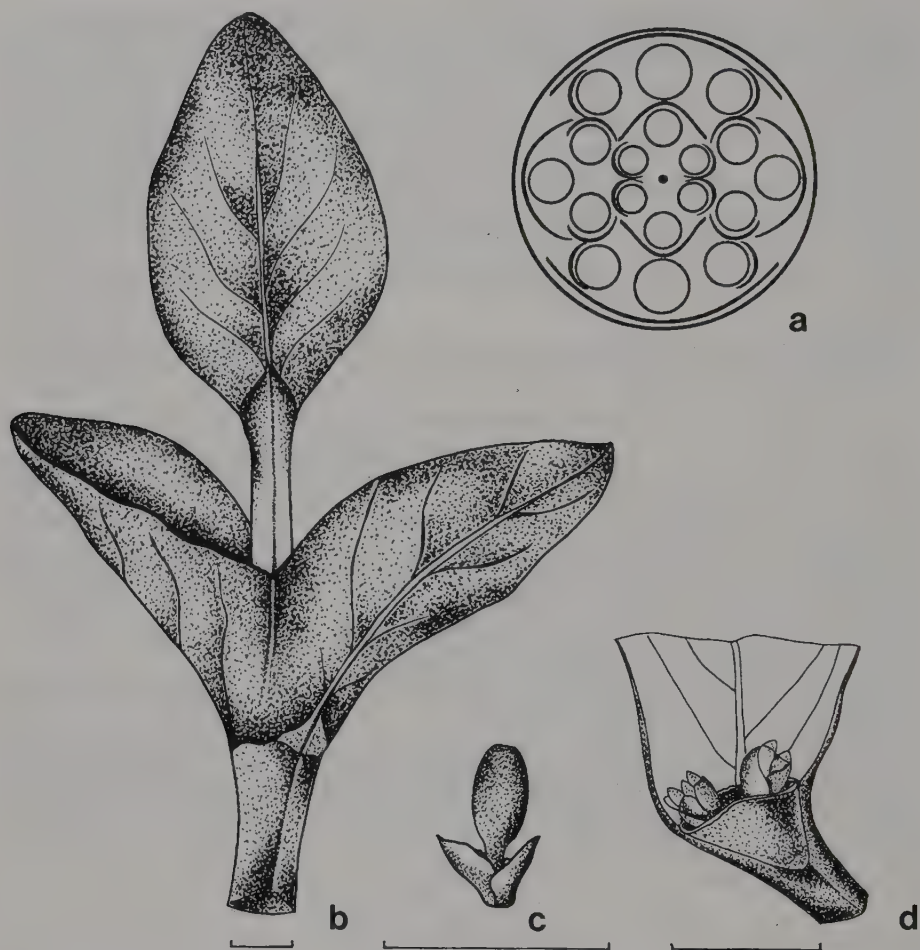


Fig. 16. *Cyne*. a. Generalized diagram of inflorescence. — *C. perfoliata* (Danser) Barlow. b. Twig with leaves; c. fruiting triad; d. stem node with one leaf removed showing young inflorescences (b–d: *Carr 14027*). a Redrawn from Danser (1933); b drawing Sandie McIntosh; c, d redrawn from Barlow (1974). Scale bars represent 1 cm.

1. *Cyne baetorta* Barlow

Cyne baetorta Barlow, *Blumea* 38 (1993) 103. — Type: *Coode 5651*, Mindoro, Suban River.

Glabrous. *Leaves* opposite; lamina elliptic, 5–7 by 3.5–5 cm, cuneate to shortly attenuate at the base to a winged petiole 4–7 mm long, rounded or obtuse at the apex, red above, pale green-brown below, dull on both sides; venation pinnate, obscure except for the dark brown midrib raised below. *Inflorescences* few in hollows at the nodes, arising through a periderm layer which remains as a basal involucre, a raceme of 2

(rarely 3) pairs of triads with the central flowers sessile and the lateral flowers shortly pedicellate; axis 3–4 mm long; peduncles of the triads c. 2 mm long; pedicels of the lateral flowers up to 0.5 mm long. *Flowers* unknown.

Distribution — *Malesia*: Philippines (Mindoro).

Habitat & Ecology — 1100–1200 m altitude; no hosts recorded.

Note — For distinction as a species see Barlow, *Blumea* 38 (1993) 103.

2. *Cyne banahaensis* (Elmer) Danser

Cyne banahaensis (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 306. — *Loranthus banahaensis* Elmer, Leaf. Philipp. Bot. 1 (1908) 288. — Type: *Elmer 9115*, lecto, Luzon, Mt Banahao. [For additional synonymy see Barlow, *Blumea* 38 (1993) 104].

Glabrous. *Leaves* opposite or displaced; lamina elliptic to ovate or obovate, 6–15 by 3.5–7(–9) cm, cuneate to attenuate at the base to a winged petiole 4–15 mm long, attenuate and obtuse or rounded at the apex, green above, brown below, dull on both sides; venation pinnate, distinct on both sides with the midrib raised below. *Inflorescences* few in hollows at the nodes, arising below a periderm layer which is usually shed, a sessile head of usually 3 pairs of triads with all flowers sessile. *Corolla* in mature bud 6-merous, 13–20 mm long, weakly inflated at the base, slender in the middle, weakly clavate and obtuse at the apex, yellow, sometimes red above; petals in the open flower coherent in the lower 2–5 mm. *Anther* 3–3.5 mm long, acute.

Distribution — *Malesia*: Philippines (Luzon, Samar, Mindanao).

Habitat & Ecology — 0–1100 m altitude; no hosts recorded.

Note — For relationships and distinction as a species see Barlow, *Blumea* 38 (1993) 104.

3. *Cyne monotrias* Barlow

Cyne monotrias Barlow, *Blumea* 38 (1993) 105. — Type: *Eyma 2655*, Ceram.

Glabrous. *Leaves* opposite; lamina elliptic, 4.5–6 by 2.5–3 cm, cuneate at the base to a winged petiole 8–12 mm long, rounded or obtuse at the apex, darker above than below, dull on both sides; venation pinnate, obscure above and distinct below. *Inflorescences* few in hollows at the nodes, arising through a periderm layer which remains as a basal involucre, a condensed spike of 1 (rarely 2) sessile triads with all flowers sessile; axis c. 1 mm long. *Corolla* in mature bud 6-merous, c. 13 mm long, weakly inflated at the base, slender in the middle, yellow; petals in the open flower coherent in the lower part. Other flower characters unknown.

Distribution — *Malesia*: Moluccas (Ceram).

Habitat & Ecology — The recorded host is a species of *Euphorbiaceae*.

Note — For discussion of morphology and distinction as a species see Barlow, *Blumea* 38 (1993) 105.

4. *Cyne papuana* (Danser) Barlow

Cyne papuana (Danser) Barlow, *Blumea* 38 (1993) 106. — *Amylothea papuana* Danser, *Blumea* 3 (1938) 38. — *Decaishina papuana* (Danser) Barlow, *Austral. J. Bot.* 22 (1974) 540; in *Handb. Fl. Papua New Guinea* 2 (1981) 238. — Type: *Carr 15502*, Papua New Guinea, Isuarava.

Glabrous. Stem internodes dilated upwards and 2-edged when young. *Leaves* opposite, sessile; lamina elliptic, c. 8 cm long, 4–5 cm wide, truncate to shortly cuneate at the base, rounded or obtuse at the apex, slightly glossy above, dull below; venation pinnate, obscure except for the midrib raised below. *Inflorescences* few at the nodes, arising through a periderm layer which remains as a basal involucre, a raceme of 1 or 2 pairs of triads with the central flowers sessile and the lateral flowers very shortly pedicellate; axis 2–4 mm long; peduncles of the triads c. 1 mm long; pedicels of the lateral flowers up to 0.5 mm long. *Corolla* in mature bud 6-merous, c. 30 mm long, pale green below, red above. Other flower characters unknown.

Distribution — *Malesia*: New Guinea, only known from the type collection.

Habitat & Ecology — 1375 m altitude; no host recorded.

Note — For discussion of morphology and taxonomic position see Barlow, *Blumea* 38 (1993) 105.

5. *Cyne perfoliata* (Danser) Barlow

Cyne perfoliata (Danser) Barlow, *Blumea* 3 (1993) 106. — *Tetradyas perfoliata* Danser, *Bull. Jard. Bot. Buitenzorg III*, 11 (1931) 362; Barlow, *Austral. J. Bot.* 22 (1974) 552; in *Handb. Fl. Papua New Guinea* 2 (1981) 254. — Type: *Forbes 299*, Papua New Guinea, Sogeri.

Glabrous. Stem internodes slightly 2-edged when young. *Leaves* opposite, sessile, those of each pair fused at the margins in the lower 1.5–2 cm into a sheath which completely encircles the stem and encloses the inflorescences; lamina ovate, c. 10 cm long, c. 6 cm wide, rounded or obtuse at the apex, slightly lustrous above, dull below; venation pinnate, distinct on both sides. *Inflorescences* few at the nodes, apparently arising through a periderm layer which remains as a basal involucre, a subsessile head of a few pairs of triads or dyads; peduncles of the triads or dyads obscure but reaching c. 1 mm in fruit; pedicels of the flowers obscure but reaching c. 1.5 mm in fruit. *Corolla* not seen mature, pale pinkish yellow. — **Fig. 16 b–d.**

Distribution — *Malesia*: New Guinea (Papua New Guinea: Central Province).

Habitat & Ecology — 960–1500 m altitude; no hosts recorded.

Notes — 1. For discussion of morphology and taxonomic position see Barlow, *Blumea* 38 (1993) 106.

2. An unusual and apparently rare species; assessment of its conservation status is needed.

6. *Cyne quadriangula* Danser

Cyne quadriangula Danser, *Philipp. J. Sc.* 58 (1935) 38. — Type: *Ramos & Pascasio BS 35119* (not located), Mindanao, Bucas Grande I.

Glabrous. Stem internodes quadrangular when young. *Leaves* opposite; lamina oblong to elliptic, 8–14 by 3.5–5 cm, truncate to shortly cuneate at the base to a petiole 6–14 mm long, shortly acuminate and obtuse at the apex, dull on both sides; venation pinnate, the midrib and main laterals distinct. *Inflorescences* few in hollows at the nodes, arising below a periderm layer which is usually shed. *Corolla* chocolate-coloured. Other characters unknown.

Distribution — *Malesia*: Philippines (Mindanao: Bucas Grande I.).

Habitat & Ecology — Low altitude; no hosts recorded.

Note — A doubtful species with no specimens extant, very similar to *Cyne banahaensis*; for discussion see Barlow, *Blumea* 38 (1993) 107.

DACTYLIOPHORA

Dactyliophora Tiegh., Bull. Soc. Bot. France 41 (1894) 549. — Type species: *Dactyliophora verticillata* (Scheff.) Tiegh.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 355].

Aerial stem-parasitic shrubs with epicortical runners bearing secondary haustoria. *Leaves* opposite or ternate. *Inflorescences* axillary or borne on the epicortical runners, consisting of 1–4 whorls of dichasia (triads) in racemose order on a common axis; triads pedunculate, with the central flower sessile and the lateral flowers pedicellate; bracts solitary under each flower. *Corolla* usually 6-merous, choripetalous, regular. *Anthers* basifixed, immobile. *Style* simple, with a knob-like stigma. *Fruit* ellipsoid or ovoid. — **Fig. 17.**

Distribution — Genus of 2 species distributed in Ceram and New Guinea, and extending beyond Malesia to Queensland (Cape York Peninsula) and the Solomon Islands.

Habitat & Ecology — Closed humid lowland forests. Host specificity is probably low.

Morphology & Taxonomy — Closely related to *Amyema*. When the inflorescence is occasionally reduced to a single node, it is essentially an umbel of triads, which is the basic inflorescence structure in *Amyema*. For further discussion, see Barlow, *Austral. J. Bot.* 22 (1974) 558.

KEY TO THE SPECIES

- 1a. Leaves opposite or ternate, rounded at the apex, mostly less than 10 cm long; inflorescence axis 2–3 mm thick **1. *D. novaeguineae***
- b. Leaves opposite, acute and more or less acuminate at the apex, mostly more than 10 cm long; inflorescence axis 1–2 mm thick **2. *D. verticillata***

1. *Dactyliophora novaeguineae* (F.M. Bailey) Danser

Dactyliophora novaeguineae (F.M. Bailey) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 307; Barlow, *Austral. J. Bot.* 22 (1974) 558; in *Handb. Fl. Papua New Guinea* 2 (1981) 231. — *Loranthus novae-guineae* F.M. Bailey, *Contr. Fl. New Guinea reimpr. ex Rep. Brit. New Guinea* (1902) 3. — Type: *Le Hunte s.n.*, Goodenough I.

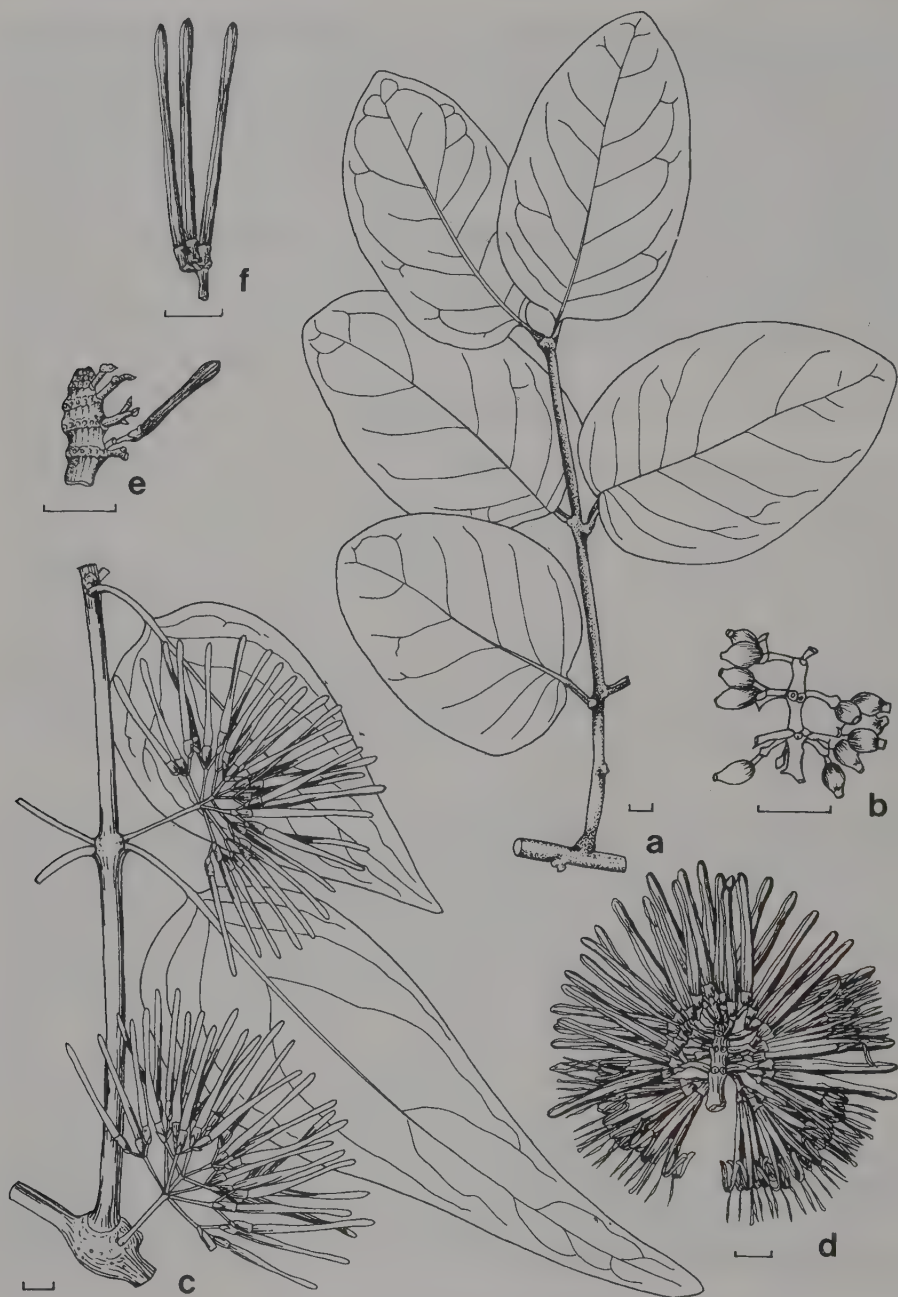


Fig. 17. *Dactyliophora novaeguineae* (F.M. Bailey) Danser. a. Twig with leaves; b. infructescence. — *D. verticillata* (Scheff.) Tiegh. c. Flower-bearing twig; d. inflorescence; e. inflorescence axis; f. triad of flower buds (a: not cited; b: *Le Hunte* s.n.; c: *Kajewski* 2497; d: *Mayr* 232; e: probably *Zippel* s.n.; f: *Docters van Leeuwen* 9477). a Redrawn from Barlow (1981), b, d–f redrawn from Danser (1931), c redrawn from Danser (1935). Scale bars represent 1 cm.

Glabrous except for the inflorescence, calyx and usually the corolla shortly brown tomentose. *Leaves* opposite or rarely scattered ternate; lamina elliptic to ovate or almost orbicular, 5–10(–15) by 3.5–7(–12) cm, cuneate at the base to a petiole 8–20 mm long, rounded or obtuse at the apex, dull or slightly lustrous above, dull and usually paler below; venation pinnate with the midrib and the main laterals distinct on both sides and the midrib prominent below. *Inflorescences* at the nodes, a raceme with usually 3 whorls of triads; axis 15–35 mm long, usually 2–3 mm thick, flowerless in the lower (8–)12–20 mm; triads at the first node mostly 8–12, at the second node mostly 8–10, at the third node (4–)6–8(–10); peduncles of the triads 5–8 mm long; pedicels of the lateral flowers c. 2 mm long. *Corolla* in mature bud 6-merous, 25–36 mm long, cylindric, acute at the apex, red or orange below, orange or yellow above. *Anther* 4–6 mm long, slightly longer than the free part of the filament. — **Fig. 17a, b.**

Distribution — Australia (Cape York Peninsula); *Malesia*: New Guinea.

Habitat & Ecology — Closed and open humid forests, 0–100 m altitude; recorded hosts include *Hibiscus*, *Intsia*, *Mallotus*, *Maniltoa*, *Rhizophora*, and *Serianthes*.

2. *Dactyliophora verticillata* (Scheff.) Tiegh.

Dactyliophora verticillata (Scheff.) Tiegh., Bull. Soc. Bot. France 41 (1894) 550; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 359; Barlow, Austral. J. Bot. 22 (1974) 560; in Handb. Fl. Papua New Guinea 2 (1981) 233. — *Dendrophthoe verticillata* Scheff., Ann. Jard. Bot. Buitenzorg 1 (1876) 27. — Type: *Teijsmann 7591*, Irian Jaya, Doreh.

Dactyliophora salomoniana Danser, J. Arnold Arbor. 16 (1935) 206; Barlow, Austral. J. Bot. 22 (1974) 559; in Handb. Fl. Papua New Guinea 2 (1981) 233. — Type: *Kajewski 2497*, Guadalcanal, Mt Tutuke.

[For additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 560].

Glabrous except for the inflorescence, calyx and corolla shortly white to brown tomentose. *Leaves* opposite; lamina elliptic to ovate, 8–30 by 4–12 cm, mostly truncate to weakly cordate at the base to a petiole 10–30 mm long, attenuate or acuminate and acute at the apex, dull or slightly lustrous on both sides, often paler below; venation pinnate with the midrib and the main laterals distinct on both sides and the midrib prominent below. *Inflorescences* at the nodes and on the epicortical runners, a raceme with 1–5 whorls of triads, these sometimes condensed together or displaced into spirals; axis variable, 5–35 mm long, 1–2 mm thick, flowerless in the lower 3–30 mm; triads at the first node 8–10, at the second node (when present) 4–12, at the third node (when present) c. 10, at the fourth and fifth nodes (when present) 4–6; peduncles of the triads 3–10 mm long; pedicels of the lateral flowers 1–3 mm long. *Corolla* in mature bud usually 6-merous, less frequently 5- to 8-merous, 25–50 mm long, slender, weakly clavate and acute at the apex, red, pink, orange or yellow below, paler and yellowish or greenish above. *Anther* 2.5–5 mm long, mostly equal to or slightly longer than the free part of the filament. — **Fig. 17c–f.**

Distribution — Solomon Islands; *Malesia*: Ceram, New Guinea.

Habitat & Ecology — Humid forests from 0 to 1200 m altitude; recorded hosts include *Albizia*, *Erythrina*, and *Ficus*.

Note — Barlow in Austral. J. Bot. 22 (1974) 559 recognized *Dactyliophora verticillata* and *D. salomonina* as distinct species. Additional materials examined show that there is no sharp morphological distinction between the two, and they are here treated as conspecific. The resultant species is relatively uniform vegetatively, although rather polymorphic in inflorescence characters. Specimens from New Britain and the Solomon Islands often have long slender inflorescences with only one whorl of triads.

DECAISNINA

Decaisnina Tiegh., Bull. Soc. Bot. France 42 (1895) 434, 435. — Type species: *Decaisnina glauca* Tiegh. [= *D. triflora* (Span.) Tiegh.].

[For additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 535; in Fl. Austral. 22 (1984) 74].

Aerial stem-parasitic shrubs, often robust, with epicortical runners bearing secondary haustoria. *Leaves* mostly opposite; venation pinnate. *Inflorescences* axillary or rarely terminal, a raceme of decussate pairs of pedunculate dichasia (triads); bracts single under each flower. *Corolla* 6- (rarely 5-)merous, regular, choripetalous although mostly with the petals weakly coherent in the lower part after anthesis. *Anthers* basifixed, immobile. *Style* simple, often articulate above the base, usually with a small knob-like stigma. *Fruit* ellipsoid, usually with a persistent nipple-like style base. — **Fig. 18, 19.**

Distribution — 25 species distributed from Java, Celebes and the Philippines south-eastwards to Australia and the Pacific as far as the Marquesas. In *Malesia* 21 species, with centres of species richness and diversity in the Philippines and New Guinea.

Habitat — Humid and open forests, mostly in lowlands, but with some species reaching altitudes of 2900 m.

Ecology — In Malesia some species are aggressive, with broad host ranges, sometimes occurring on cultivated trees.

Morphology — In many *Decaisnina* species the inflorescence is presented horizontally and the triads are secund, all turning upwards on their peduncles so that the inflorescence has a brush-like appearance. In some species the short corolla tube formed by the coherent petals is dilated to form a distinct nectar chamber.

Taxonomy — Circumscription of generic limits of *Decaisnina* and related genera has proved difficult, and has been revised progressively by Danser and then Barlow. Danser in his revisions included *Decaisnina* in *Amylothea*, with some reservations, thus circumscribing the latter genus more broadly than here. For a conspectus of these and related genera see Barlow, *Blumea* 38 (1993) 65–126.

KEY TO THE SPECIES

- 1a. Inflorescence subtended by an involucre of decussate scales at the base of the axis 2
- b. Inflorescence not subtended by an involucre of decussate scales at the base of the axis 6

- 2a. Inflorescence axis oriented vertically with the flowers not strongly secund; lateral flowers of the triads on distinct pedicels at least as long as the ovary 3
 - b. Inflorescence axis oriented horizontally with the flowers strongly secund, giving the inflorescence a brush-like appearance; lateral flowers of the triads on obscure pedicels much shorter than the ovary 5
- 3a. Stems and inflorescence parts very thick; internodes short and often crowded so that the leaves appear verticillate; corolla more than 30 mm long **20. D. viridis**
 - b. Stems and inflorescence parts slender to moderately robust; internodes normally developed with evenly spaced decussate leaf pairs; corolla less than 30 mm long 4
- 4a. Inflorescence axis less than 15 mm long; corolla 5-merous, hardly inflated at the base **14. D. ovatifolia**
 - b. Inflorescence axis more than 30 mm long; corolla 6-merous, distinctly inflated at the base **1. D. aherniana**
- 5a. Leaf lamina up to 8 cm long; triads crowded at the end of the inflorescence axis **16. D. revoluta**
 - b. Leaf lamina more than 10 cm long; triads distributed uniformly along the inflorescence axis **6. D. crassilimba**
- 6a. Anthers sessile or nearly so, with free filament less than 1 mm long 7
 - b. Anthers on distinct free filaments at least 2 mm long 9
- 7a. Corolla less than 10 mm long **12. D. micranthes**
 - b. Corolla 10–24 mm long 8
 - c. Corolla more than 24 mm long **13. D. miniata**
- 8a. Young internodes 4-angular; leaf lamina glossy on both sides, darker above, recurved at the margin; inflorescence and flowers shortly and densely tomentose **4. D. confertiflora**
 - b. Young internodes dilated and 2-angled in the upper part; leaf lamina dull on both sides, not recurved at the margin; inflorescence and flowers glabrous or sparsely hairy **7. D. cumingii**
- 9a. Triads in 1–3 pairs crowded near the apex of the inflorescence axis 10
 - b. Triads in several pairs distributed uniformly along much of the inflorescence axis 12
- 10a. Stems and inflorescence parts very thick; internodes short and often crowded so that the leaves appear verticillate; corolla inflated to 5 mm wide in the lower part **20. D. viridis**
 - b. Stems and inflorescence parts slender to robust; internodes normally developed with evenly spaced decussate leaf pairs; corolla not or slightly inflated at the base 11
- 11a. Leaf lamina acuminate acute at the apex; corolla 35–50 mm long **3. D. celebica**
 - b. Leaf lamina obtuse to rounded at the apex, often with a small blunt mucro; corolla 23–30 mm long **5. D. congesta**
- 12a. Leaves with upper surface glossy or darker than the dull lower surface 13
 - b. Leaves dull and more or less the same colour on both sides 16
- 13a. Leaves sessile, truncate to amplexicaul at the base **2. D. amplexicaulis**
 - b. Leaves petiolate, or if sessile attenuate at the base 14

- 14a. Petals eventually separating to the base; anthers transversely septate prior to anthesis **9. *D. forsteriana***
- b. Petals remaining coherent in the lower part; anthers not transversely septate ... 15
- 15a. Plant robust, usually with a short brown tomentum on the young parts and inflorescences; leaves with a distinct petiole mostly more than 10 mm long; corolla mostly more than 30 mm long **10. *D. hollrungii***
- b. Plant relatively slender, glabrous or rarely with the inflorescence sparsely pubescent; leaves with a petiole mostly less than 10 mm long; corolla less than 30 mm long **18. *D. sumbawensis***
- 16a. Corolla inflated and globular at the base 17
- b. Corolla not inflated at the base, or if so then not sharply contracted to form a globular dilation 18
- 17a. Young internodes strongly angular distally **21. *D. zollingeri***
- b. Young internodes not strongly angular distally **17. *D. stenopetala***
- 18a. Corolla pale green or yellow in the lower part; petals separating to the base at anthesis **8. *D. djamuensis***
- b. Corolla red in the lower part; petals cohering in the lower 1–15 mm after anthesis 19
- 19a. Triads with all flowers sessile **19. *D. triflora***
- b. Triads with the central flower sessile and the lateral flowers pedicellate 20
- 20a. Leaf lamina broadly lanceolate to elliptic, attenuate at the base to an obscure petiole 3–5 mm long; corolla 23–30 mm long **15. *D. pedicellata***
- b. Leaf lamina elliptic to almost orbicular, shortly cuneate at the base with a distinct petiole 25–40 mm long; corolla 30–50 mm long **11. *D. longipes***

1. *Decaisnina aherniana* (Merr.) Barlow

Decaisnina aherniana (Merr.) Barlow, Blumea 38 (1993) 74. — *Loranthus ahernianus* Merr., Philipp. J. Sc. 1, Suppl. (1906) 184. — *Amylothea aherniana* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 300. — Type: *Ahern's Collector FB 2140*, lecto, Luzon, Bosoboso.
 [For additional synonymy see Barlow, Blumea 38 (1993) 74].

Glabrous except for young inflorescences sometimes shortly pubescent. *Leaves* opposite (sometimes displaced); lamina lanceolate to ovate, mostly 6–16 cm long, mostly 2–6 cm wide, shortly cuneate to cordate at the base to a petiole 4–14 mm long, acute and often acuminate at the apex, glossy above, dull below; venation pinnate with the midrib prominent and the main laterals visible on both sides. *Inflorescences* at the nodes, a raceme of 5–16 opposite evenly spaced pairs of triads with the central flower sessile and the lateral flowers pedicellate; axis 36–90 mm long, subtended at the base by an involucre of 3–6 pairs of triangular keeled bracts up to 4 mm long; peduncles of the triads 5–12 mm long, usually not secund; pedicels of the lateral flowers 2.5–8 mm long. *Corolla* in mature bud 6-merous, 14–29 mm long, inflated at the base, clavate and obtuse at the apex, mostly white or yellow, rarely red; petals in the open flower separating to the base or coherent in the lower 5 mm. *Anther* 1.5–4 mm long, about half as long as the free part of the filament.

Distribution — *Malesia*: Philippines.

Habitat & Ecology — Humid forests from 0 to 1200 m altitude; recorded hosts include *Litsea*, *Semecarpus*, and *Syzygium*.

Note — Closely related to *Decaisnina ovatifolia*; for differences and distinction as a species see Barlow, *Blumea* 38 (1993) 75, 91.

2. *Decaisnina amplexicaulis* (Danser) Barlow

Decaisnina amplexicaulis (Danser) Barlow, *Blumea* 38 (1993) 76. — *Amylothea amplexicaulis* Danser, Philipp. J. Sc. 58 (1935) 14. — Type: *Ramos & Edaño BS 38740*, lecto, Mindanao, Mt Candon.

Glabrous. *Leaves* opposite; lamina ovate, 4–12 by 2–5 cm, weakly cordate at the base, sessile, rounded to acuminate and acute at the apex, somewhat glossy above, dull below; venation pinnate with the midrib prominent on both sides and the main laterals distinct above. *Inflorescences* at the nodes, a raceme of 5–10 opposite evenly spaced pairs of triads with all flowers sessile or the lateral flowers shortly pedicellate; axis 30–55 mm long; peduncles of the triads 1–2 mm long, secund; pedicels of the lateral flowers 0–0.5 mm long. *Corolla* in mature bud 6-merous, c. 33 mm long, slender above a rounded base, clavate and obtuse at the apex, purplish red below, white at the neck and light green above; petals in the open flower separating to the base. *Anther* 2.5–4 mm long, about equal to the free part of the filament. — **Fig. 18a, b.**

Distribution — *Malesia*: Philippines (Mindanao), New Guinea (Bird's Head Peninsula).

Habitat & Ecology — 230–1500 m altitude; no hosts recorded.

Note — For distinction as a species, see Barlow, *Blumea* 38 (1993) 76.

3. *Decaisnina celebica* (Hemsl.) Barlow

Decaisnina celebica (Hemsl.) Barlow, *Blumea* 38 (1993) 80. — *Loranthus celebicus* Hemsl., Kew Bull. (1896) 39. — *Amylothea celebica* (Hemsl.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 300. — Type: *Everett s.n.*, Celebes, Bonthain Peak (= Mt Lompobatang).

Glabrous. *Leaves* opposite; lamina lanceolate to ovate, 4–8 by 2–3 cm, attenuate at the base to a petiole 3–7 mm long, acuminate and acute at the apex, weakly glossy above, dull below; venation pinnate with the midrib prominent and the main laterals visible on both sides. *Inflorescences* at the nodes, a raceme of 3–5 opposite pairs of triads with all flowers sessile; axis 20–34 mm long, lacking triads in the lower (12–)16–24 mm; peduncles of the triads 2–4 mm long, secund. *Corolla* in mature bud 6-merous, 39–49 mm long, slender, weakly clavate and acute at the apex, red below and yellow above; petals in the open flower coherent in the lower 10 mm. *Anther* c. 7 mm long, about equal to the free part of the filament.

Distribution — *Malesia*: Celebes (Mt Lompobatang).

Habitat & Ecology — 2000–2850 m altitude; no hosts recorded.

Note — Related to *Decaisnina sumbawensis*; also similar to *D. congesta*; for discussion see Barlow, *Blumea* 38 (1993) 80.

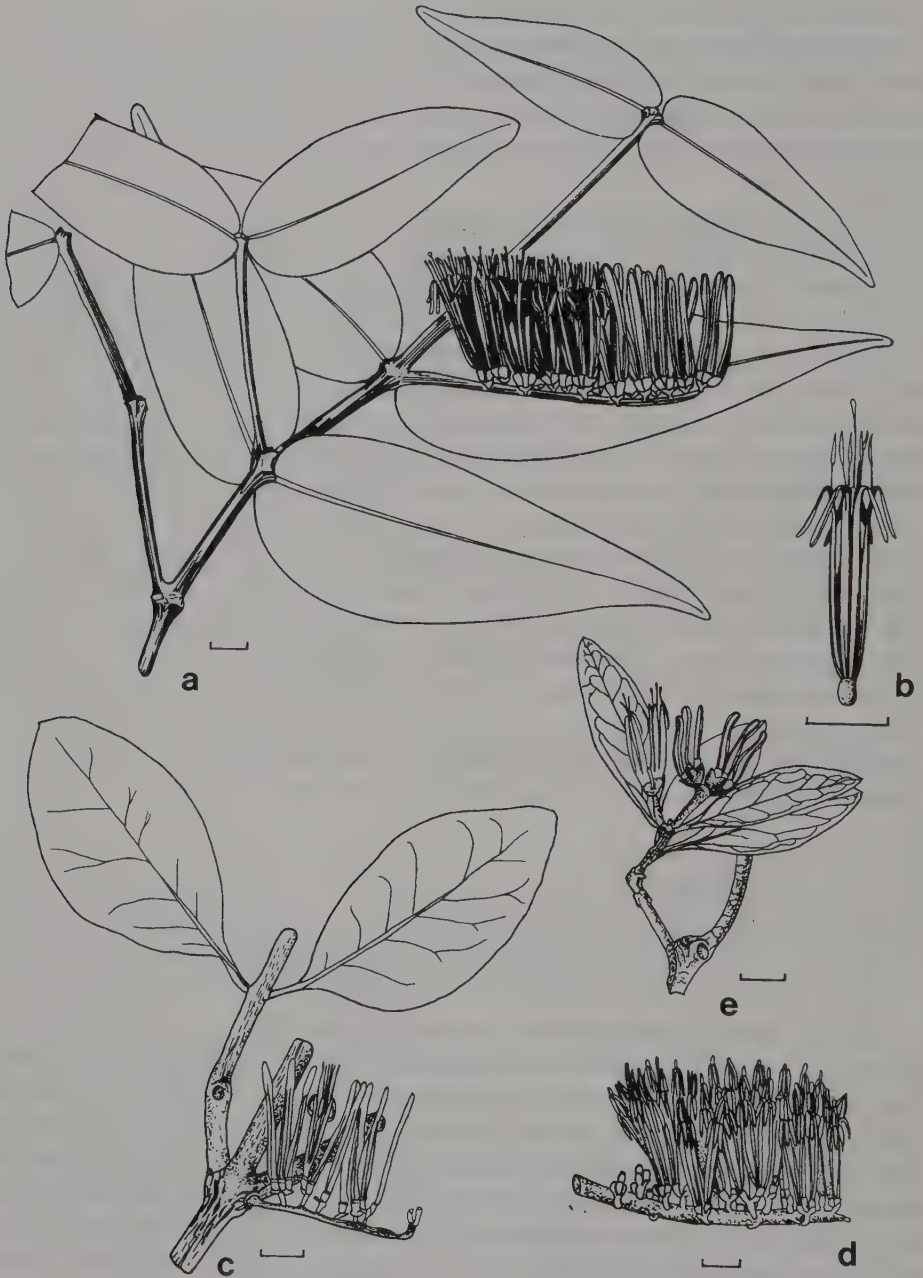


Fig. 18. *Decaisnina amplexicaulis* (Danser) Barlow. a. Flower-bearing twig; b. flower. — *D. hollrungii* (K. Schum.) Barlow. c. Flower-bearing twig; d. inflorescence. — *D. congesta* Barlow. e. Flower-bearing twig (a, b: Ramos & Edaño BS 38740; c: Barlow 3719; d: not cited; e: Gray 1168). a, b Redrawn from Danser (1935), c, e redrawn from Barlow (1984); d redrawn from Barlow (1981). Scale bars represent 1 cm.

4. *Decaisnina confertiflora* (Merr.) Barlow

Decaisnina confertiflora (Merr.) Barlow, *Blumea* 38 (1993) 80. — *Loranthus confertiflorus* Merr., Philipp. J. Sc., Bot. 13 (1918) 273. — *Amylothea confertiflora* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 300. — Type: *Wenzel 1249*, lecto, Leyte; see note 3.

Glabrous except for the inflorescences shortly and densely off-white tomentose and the young flowers sparsely so. Stem internodes distinctly 4-angular. *Leaves* opposite; lamina narrowly ovate, 12–20 by 5–8 cm, truncate or slightly cordate at the base to a petiole 12–15 mm long, acuminate and acute at the apex, glossy on both sides, darker above; venation pinnate with the midrib distinct above and prominent below and the main laterals faintly visible on both sides. *Inflorescences* at the nodes, a raceme of 10–15 opposite evenly spaced crowded pairs of triads with all flowers sessile; axis 20–30 mm long; peduncles of the triads 1–2 mm long, secund. *Corolla* in mature bud 6-merous, 16–20 mm long, slightly inflated at the base for 2–3 mm, slender above, weakly clavate and broadly acute or obtuse at the apex, red; petals in the open flower coherent in the inflated part. *Anther* c. 2 mm long, acute, much longer than the free part of the filament (subsessile).

Distribution — *Malesia*: Philippines (Leyte).

Habitat & Ecology — No data.

Notes — 1. Similar to *Decaisnina sumbawensis*, differing in angular stems, slightly cordate leaf lamina base, tomentose inflorescence, shorter corolla and subsessile anthers.

2. Barlow, in *Blumea* 38 (1993) 81, reported that no specimens had been located and treated the species as doubtful. Specimens subsequently located (see below) have confirmed the status of the species, and resulted in the amended description above.

3. The holotype of *Loranthus confertiflorus* Merr. (PNH) is no longer extant. An isotype in GH has been seen and identified as lectotype of the name, and other isotypes have been seen in GH, MO and NSW.

5. *Decaisnina congesta* Barlow

Decaisnina congesta Barlow, *Brunonia* 5 (1983) 204. — Type: *Gray 1168*, Queensland.

Glabrous. *Leaves* opposite; lamina elliptic, 5–8 by 2–4 cm, cuneate at the base to a distinct petiole 6–10(–15) mm long, obtuse or rounded at the apex with a small blunt mucro, dull on both sides but slightly darker above; venation pinnate with the midrib and the main laterals visible above and prominent below. *Inflorescences* at the nodes, a subcapitate raceme of 1–3 opposite pairs of triads with all flowers sessile; axis 8–13 mm long, with the triads crowded near the apex; peduncles of the triads 0–1 mm long, secund. *Corolla* in mature bud 6-merous, 23–30 mm long, slender, acute at the apex, mostly red below and green above; petals in the open flower coherent in the lower 2–5 mm. *Anther* 2.5–3.5 mm long, acute, about equal to the free part of the filament. —

Fig. 18e.

Distribution — Queensland; *Malesia*: New Guinea.

Habitat & Ecology — Humid and open forests from 0 to 1875 m altitude; recorded hosts include *Alstonia*, *Engelhardtia*, and *Morus*.

Note — Possibly related to *Decaisnina triflora*; for distinction as a species see Barlow, Blumea 38 (1993) 81.

6. *Decaisnina crassilimba* (Merr.) Barlow

Decaisnina crassilimba (Merr.) Barlow, Blumea 38 (1993) 82. — *Loranthus crassilimbus* Merr., Philipp. J. Sc., Bot. 13 (1918) 274. — *Amylothea crassilimba* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 300. — Type: *Ramos & Edaño BS 26409*, lecto, Luzon, Mt Umingan.

Glabrous. *Leaves* opposite; lamina elliptic to ovate, 10–20 by 4–10 cm, shortly cuneate or truncate at the base to a distinct petiole 20–30 mm long, obtuse at the apex, glossy green above, dull red-brown below; venation pinnate with the midrib very prominent below and the main laterals obscure on both sides. *Inflorescences* at the nodes, a raceme of c. 9 opposite evenly spaced pairs of triads with the central flower sessile and the lateral flowers shortly pedicellate or subsessile; axis 30–65 mm long, subtended at the base by an involucre of several pairs of scarious broadly triangular bracts up to 6 mm long; peduncles of the triads 4–10 mm long, secund; pedicels of the lateral flowers 0.5–1.5 mm long. *Corolla* in mature bud 6-merous, 22–33 mm long, moderately robust, weakly clavate and obtuse at the apex, mostly red or yellow below and yellow or green above; petals in the open flower separating completely or almost to the base. *Anther* 3.5–5 mm long, acute, 3–4 times as long as the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon, Panay).

Habitat & Ecology — 300–1400 m altitude; no hosts recorded.

Note — For distinction as a species and taxonomic position, see Barlow, Blumea 38 (1993) 82.

7. *Decaisnina cumingii* (Tiegh.) Barlow

Decaisnina cumingii (Tiegh.) Barlow, Blumea 38 (1993) 82. — *Amylothea cumingii* Tiegh., Bull. Soc. Bot. France 41 (1894) 264. — Type: *Cuming 1969*, Philippines, 'Manille'.
[For additional synonymy see Barlow, Blumea 38 (1993) 82].

Glabrous except for young inflorescence parts sometimes shortly hairy. *Leaves* opposite or scattered; lamina mostly narrowly elliptic to ovate, 5–10(–14) cm long, mostly 3–6 cm wide, usually attenuate or cuneate at the base to a petiole up to 15 mm long, less commonly truncate or slightly cordate and more or less sessile, mostly somewhat attenuate and finally rounded at the apex, dull on both sides, sometimes darker above; venation pinnate with the midrib prominent below and the main laterals visible on both sides. *Inflorescences* at the nodes, a raceme of (2–)3–7 opposite pairs of triads with all flowers sessile; axis (17–)25–70 mm long, flowerless in the lower (5–)10–20 mm; peduncles of the triads 0–4 mm long, secund. *Corolla* in mature bud 6- (rarely 5-)merous, (11–)13–19(–21) mm long, usually dilated but not globular in the lower part, moderately robust, shortly clavate and obtuse at the apex, mostly yellow or orange or red, darker below than above; petals in the open flower separating to the base or coherent in the lower 3 mm. *Anther* (1.5–)2.5–3(–4) mm long, acute, usually much longer than the free part of the filament and mostly subsessile or sessile.

Distribution — *Malesia*: Philippines, Moluccas.

Habitat & Ecology — Humid forests, 0–2300 m altitude; recorded hosts include *Kibatalia* and *Shorea*.

Note — Related to *Decaisnina zollingeri*; for differences and species circumscription see Barlow, Blumea 38 (1993) 83.

8. *Decaisnina djamuensis* (K. Krause) Barlow

Decaisnina djamuensis (K. Krause) Barlow, Austral. J. Bot. 22 (1974) 536; in Handb. Fl. Papua New Guinea 2 (1981) 234. — *Loranthus djamuensis* K. Krause, Bot. Jahrb. 57 (1922) 478. — *Amylothea djamuensis* (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 243. — Type: *Schlechter 17319*, New Guinea, Djamu (Ramu) River.

[For additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 536].

Glabrous except for the young stems and leaves brown scurfy. *Leaves* opposite; lamina narrowly ovate to ovate, 8–14 cm long, mostly 4–7 cm wide, attenuate or cuneate at the base to a distinct petiole c. 10 mm long, usually attenuate and acute to rounded at the apex, dull powdery green on both sides; venation pinnate with the brown midrib distinct and raised in the lower part and the main laterals indistinct on both sides. *Inflorescences* at the nodes, a raceme of 6–9 opposite evenly spaced pairs of triads with the central flower sessile and the lateral flowers shortly pedicellate; axis 30–60 mm long; peduncles of the triads 1–3 mm long, secund; pedicels of the lateral flowers c. 0.5 mm long but longer under the fruit; bracts rounded, imbricate, c. 2.5 mm long. *Corolla* in mature bud 6-merous, (15–)20–26 mm long, slender, rounded at the apex, mostly green (rarely red) and sometimes shading to yellow or red above; petals in the open flower separating to the base. *Anther* c. 2.5 mm long, acute, slightly longer than the free part of the filament.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Humid forests, mostly 0–200 m altitude, rarely up to 1050 m; recorded hosts include *Anisoptera*, *Cinnamomum*, and *Eucalyptopsis*.

Note — Related to *Decaisnina micranthes*; for differences see Barlow, Blumea 38 (1993) 85.

9. *Decaisnina forsteriana* (Schult. & Schult. f.) Barlow

Decaisnina forsteriana (Schult. & Schult. f.) Barlow in D. Walker (ed.), Bridge and Barrier, Austral. Nat. Univ. Publ. BG/3 (1972) 185; Barlow, Austral. J. Bot. 22 (1974) 537; in Handb. Fl. Papua New Guinea 2 (1981) 235. — *Loranthus forsterianus* Schult. & Schult. f., Syst. Veg. 7, 2 (1830) 1612, 1730. — *Amylothea forsteriana* (Schult. & Schult. f.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 301. — Type: *Forster 76*, Tahiti.

[For additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 537].

Glabrous. *Leaves* opposite; lamina narrowly ovate to broadly ovate or rhomboid, 3–7 (–9) by 2.5–5 cm, cuneate or attenuate at the base to a distinct petiole 10–20 mm long, acute to rounded at the apex, dull on both sides or darker and slightly lustrous above, thin; venation pinnate with the midrib and the main laterals usually distinct on both sides. *Inflorescences* at the nodes, a raceme of mostly 3–6 opposite evenly spaced pairs of

triads with the central flower sessile and the lateral flowers pedicellate; axis 20–30 mm long; peduncles of the triads 4–6 mm long, secund; pedicels of the lateral flowers 0.5–2 mm long. *Corolla* in mature bud 6- (rarely 5-)merous, (25–)35–50 mm long, slender, clavate and obtuse at the apex, mostly red, often darker towards the tip, but predominantly yellow in some populations; petals in the open flower usually separating to the base but sometimes long coherent in the lower 2 mm. *Anther* 2–3(–5) mm long, obtuse below a short mucro, finely transversely septate prior to anthesis, slightly shorter than the free part of the filament.

Distribution — Solomon Islands eastwards to Tahiti and the Marquesas; *Malesia*: New Guinea (Louisiade Archipelago).

Habitat & Ecology — Humid and open forests from 0 to 1900 m altitude but most common in uplands; recorded hosts include *Diospyros*, *Ficus*, *Grewia*, *Homalanthus*, *Inocarpus*, *Metrosideros*, *Pittosporum*, and *Wikstroemia*.

Notes — 1. For a discussion of taxonomic affinities see Barlow, *Blumea* 38 (1993) 87.

2. The species is exceptional in *Loranthaceae* for its wide distribution to oceanic islands; for discussion see Barlow & Schodde, *Beaufortia* 43 (1993) 124.

10. *Decaisnina hollrungii* (K. Schum.) Barlow

Decaisnina hollrungii (K. Schum.) Barlow, *Austral. J. Bot.* 14 (1966) 434; 22 (1974) 538; in *Handb. Fl. Papua New Guinea* 2 (1981) 235. — *Loranthus hollrungii* K. Schum. in K. Schum. & Holtr., *Fl. Kaiser Wilhelm Land* (1889) 105. — *Amylothea hollrungii* (K. Schum.) Tiegh., *Bull. Soc. Bot. France* 41 (1894) 263; Danser, *Bull. Jard. Bot. Buitenzorg III*, 10 (1929) 301. — Type: *Hollrung 659*, New Guinea, 'Augustafluss'.

[For additional synonymy see Barlow, *Austral. J. Bot.* 22 (1974) 538].

Glabrous except for the leaf undersides frequently and the petioles, young stems and inflorescences sometimes shortly and sparsely brown tomentose. *Leaves* opposite; lamina lanceolate to ovate, (5–)8–18(–25) by (1.5–)4–8(–12) cm, cuneate to weakly cordate at the base to a petiole 5–30 mm long, acute or obtuse at the apex, glossy above, dull below; venation pinnate with the midrib prominent below and the main laterals distinct or obscure. *Inflorescences* at the nodes, a raceme of 5–14 evenly spaced opposite pairs of triads with all flowers sessile or sometimes the lateral flowers pedicellate; axis very variable, sometimes only 12 mm long, sometimes reaching 120 mm in fruit; peduncles of the triads 1.5–8 mm long, secund; pedicels of the lateral flowers 0–3 mm long. *Corolla* in mature bud 6-merous, (25–)30–40(–60) mm long, moderately robust, weakly clavate and obtuse at the apex, variable in colour but often red below and yellow or green above; petals in the open flower coherent in the lower 1–8 mm. *Anther* 3–4(–6) mm long, acute, about equal to the free part of the filament. — **Fig. 18c, d.**

Distribution — Queensland, Solomon Islands; *Malesia*: Moluccas (Tanimbar, Kei), New Guinea.

Habitat & Ecology — Humid forests, mostly at 0–2000 m altitude, rarely to 2900 m; recorded on numerous dicotyledonous hosts, frequently on *Ficus*.

Note — For taxonomic relationships see Barlow, *Blumea* 38 (1993) 87.

11. *Decaisnina longipes* Barlow

Decaisnina longipes Barlow, Blumea 38 (1993) 87. — Type: *Ridsdale NGF 30401*, New Britain, Kilenge.

Glabrous. *Leaves* opposite; lamina elliptic to almost orbicular, 8–13 by 4.5–9 cm, cuneate at the base to a winged petiole 25–40 mm long, rounded at the apex, slightly glossy or dull above, dull below; venation pinnate with the midrib prominent below and the main laterals faintly visible on both sides. *Inflorescences* at the nodes, a raceme of 10–14 opposite pairs of triads, these often in loose whorls of 4, with the central flower sessile and the lateral flowers pedicellate; axis 35–70 mm long; peduncles of the triads 5–10 mm long, secund; pedicels of lateral flowers 1.5–3 mm long. *Corolla* in mature bud 6-merous, 30–50 mm long, slender, shortly rounded at apex, red below and yellow above; petals in the open flower coherent as a slender tube in the lower 2–15 mm. *Anther* 4–8 mm long, acute, about two or three times as long as the free part of the filament.

Distribution — *Malesia*: Northeastern New Guinea, Bismarck Archipelago.

Habitat & Ecology — Humid forests from 60 to 700 m altitude; no host records.

Note — For distinction as a species and taxonomic relationships see Barlow, Blumea 38 (1993) 88.

12. *Decaisnina micranthes* (Danser) Barlow

Decaisnina micranthes (Danser) Barlow, Austral. J. Bot. 22 (1974) 540; in Handb. Fl. Papua New Guinea 2 (1981) 237. — *Amylothea micranthes* Danser, Blumea 2 (1936) 34. — Type: *de Bruyn 369*, lecto, New Guinea, Biak I.

Glabrous except for young shoots sometimes sparsely brown tomentose. *Leaves* opposite; lamina lanceolate to elliptic, 6–8 by 2.5–4 cm, shortly cuneate at the base to a distinct petiole c. 10 mm long, sometimes attenuate but finally rounded at the apex, dull powdery green on both sides; venation pinnate with the midrib distinct and the main laterals faintly visible on both sides. *Inflorescences* at the nodes, a raceme of c. 5 opposite evenly spaced pairs of triads with the central flower sessile and the lateral flowers nearly so; axis 35–40 mm long; peduncles of the triads c. 1 mm long, secund. *Corolla* in mature bud 6-merous, 6–8 mm long, slender, weakly clavate and obtuse at apex, light green; petals in open flower separating to the base. *Anther* c. 1.5 mm long, acute, subsessile.

Distribution — *Malesia*: New Guinea (Irian Jaya: Biak I.).

Habitat & Ecology — Humid forests, 0–100 m altitude; recorded hosts include *Glochidion* and *Macaranga*.

Note — Related to *Decaisnina cumingii* and *D. djamuensis*; for differences see Barlow, Blumea 38 (1993) 89.

13. *Decaisnina miniata* (Elmer) Barlow

Decaisnina miniata (Elmer) Barlow, Blumea 38 (1993) 89. — *Loranthus miniatus* Elmer, Leaf. Philipp. Bot. 6 (1913) 1966, nom. illeg., non S. Moore (1897). — *Amylothea miniata* Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 301. — Type: *Elmer 13276*, lecto, Mindanao, Mt Urdaneta.

Glabrous. *Leaves* opposite; lamina narrowly ovate to ovate, 15–23 by 7–12 cm, cordate at the base, sessile, acuminate and acute at the apex, dull and somewhat glaucous above, dull below; venation pinnate with the midrib prominent below and the main laterals distinct on both sides, with the leaf upper surface bullate between them. *Inflorescences* at the nodes, a raceme of many opposite densely crowded pairs of triads with all flowers sessile; axis 15–30 mm long; peduncles of the triads 1–2 mm long, secund. *Corolla* in mature bud 6-merous, 25–28 mm long, slightly inflated at the base, slender, weakly clavate and obtuse at the apex, mostly red below and sometimes white and grey above; petals in the open flower coherent in the lower 1 mm. *Anther* 3–5 mm long, acute, subsessile.

Distribution — *Malesia*: Philippines (Siargao, Mindanao).

Habitat & Ecology — 0–380 m altitude; the only recorded host is *Canarium*.

14. *Decaisnina ovatifolia* (Merr.) Barlow

Decaisnina ovatifolia (Merr.) Barlow, *Blumea* 38 (1993) 90. — *Loranthus ovatifolius* Merr., *Philipp. J. Sc., Bot.* 3 (1908) 133. — *Amylothea ovatifolia* (Merr.) Danser, *Bull. Jard. Bot. Buitenzorg III*, 10 (1929) 302. — Type: *Clemens 1195*, lecto, Mindanao.

Glabrous. *Leaves* opposite; lamina narrowly ovate to ovate, 3–8 by 1–5.5 cm, truncate to cordate at the base to a petiole 3–5 mm long, acute and often acuminate at the apex, glossy above, dull below; venation pinnate with the midrib prominent and the main laterals visible on both sides. *Inflorescences* at the nodes, a raceme of about 5 opposite crowded pairs of triads with the central flower sessile and the lateral flowers pedicellate; axis 5–10 mm long, subtended at the base by an involucre of a few pairs of short triangular bracts; peduncles of the triads 1.5–3 mm long, not secund; pedicels of the lateral flowers 1–1.5 mm long. *Corolla* in mature bud 5-merous, 16–23 mm long, very weakly inflated at the base, weakly clavate and obtuse at the apex, red; petals in the open flower coherent in the lower 3–6 mm. *Anther* c. 1.5 mm long, obtuse, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Philippines (Bilar, Mindanao).

Habitat & Ecology — 0–610 m altitude; no hosts recorded.

Note — Closely related to *Decaisnina aherniana*; for differences see Barlow, *Blumea* 38 (1993) 91.

15. *Decaisnina pedicellata* (Danser) Barlow

Decaisnina pedicellata (Danser) Barlow, *Austral. J. Bot.* 22 (1974) 541; in *Handb. Fl. Papua New Guinea* 2 (1981) 239. — *Amylothea triflora* (Span.) Danser var. *pedicellata* Danser, *Blumea* 3 (1938) 39. — Type: *Carr 12077*, Papua New Guinea, Koitaki.

Glabrous. *Leaves* opposite; lamina broadly lanceolate to elliptic, somewhat falcate, 7–10 by 1.5–3.5 cm, cuneate at the base to a petiole 3–5 mm long, attenuate and obtuse or rounded at the apex, dull on both sides; venation pinnate with the midrib and the closely spaced main laterals distinct on both sides. *Inflorescences* at the nodes, a raceme

of c. 4 opposite closely spaced pairs of triads with the central flower sessile and the lateral flowers pedicellate; axis c. 10 mm long; peduncles of the triads c. 2 mm long, secund; pedicels of the lateral flowers c. 1 mm long. *Corolla* in mature bud 6-merous, 25–28 mm long, slender, acute at the apex, pale pink to purple, sometimes darker below; petals in the open flower coherent in the lower 2–3 mm. *Anther* c. 1.5 mm long, acute, about one third as long as the free part of the filament.

Distribution — *Malesia*: Papua New Guinea (Sogeri Plateau).

Habitat & Ecology — 425–600 m altitude; the only recorded host is *Engelhardtia*.

Note — Probably related to *Decaisnina triflora*; for comparison see Barlow, *Blumea* 38 (1993) 92.

16. *Decaisnina revoluta* (Merr.) Barlow

Decaisnina revoluta (Merr.) Barlow, *Blumea* 38 (1993) 92. — *Loranthus revolutus* Merr., Philipp. J. Sc., Bot. 4 (1909) 142. — *Amylothea revoluta* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 302. — Type: *Ramos BS 4785*, lecto, Luzon, Mt Tapulao.

Glabrous. *Leaves* opposite; lamina elliptic, 5–8 by 2–3.5 cm, attenuate or cuneate at the base to a winged petiole c. 10 mm long, obtuse at the apex, glossy and somewhat glaucous above, dull brownish below; venation regularly pinnate with the midrib and the main laterals distinct above and prominent below. *Inflorescences* at the nodes, a raceme of about 4 opposite subcapitate pairs of triads with the central flower sessile and the lateral flowers pedicellate; axis 30–35 mm long; peduncles of the triads c. 2 mm long, secund; pedicels of the lateral flowers c. 1 mm long. *Corolla* in mature bud 6-merous, 22–25 mm long, weakly inflated at the base, weakly clavate and obtuse at the apex, yellow below and red above; petals in the open flower separating to the base or shortly and weakly coherent. *Anther* c. 3 mm long, acute, slightly longer than the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — Highlands, recorded at 2100 m altitude; no host recorded.

Note — Related to *Decaisnina crassilimba*; for differences see Barlow, *Blumea* 38 (1993) 93.

17. *Decaisnina stenopetala* (Oliver) Barlow

Decaisnina stenopetala (Oliver) Barlow, Austral. J. Bot. 22 (1974) 543; in Handb. Fl. Papua New Guinea 2 (1981) 239. — *Loranthus stenopetalus* Oliver, J. Linn. Soc. 15 (1877) 99. — *Amylothea stenopetala* (Oliver) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 302. — Type: *Riedel s.n.*, Celebes, Gorontalo.

Glabrous. *Leaves* opposite; lamina narrowly ovate to ovate, 6–16 by 2–6 cm, usually attenuate to cuneate at the base to a petiole 5–10 mm long, attenuate or acuminate and acute or obtuse at the apex, thin and wrinkled and fragile when dry, dull on both sides or very slightly darker and more lustrous above; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes, a raceme of 3–6 opposite evenly spaced pairs of triads with all flowers sessile; axis 20–40 mm long; pe-

duncles of the triads 0.5–1.5 mm long, secund. *Corolla* in mature bud 6-merous, 22–30 mm long, inflated at the base, slender in the middle, weakly clavate and obtuse at the apex, mostly red below and yellow or green above; petals in the open flower separating to the inflated basal part. *Anther* 3–4 mm long, acute, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Celebes, Lesser Sunda Islands, Moluccas, New Guinea (Bird's Head Peninsula).

Habitat & Ecology — Primary and disturbed humid forests, mostly from 0 to 500 m altitude, sometimes up to 1400 m; recorded hosts include *Aglaia*, *Citrus*, *Euodia*, *Euphorbia*, *Ficus*, *Gnetum*, and *Weinmannia*.

Notes — 1. Closely related to *Decaisnina sumbawensis* and *D. zollingeri*; for comparison see Barlow, *Blumea* 38 (1993) 94.

2. The inflation of the corolla base may be transient, at anthesis, and not consistently visible.

18. *Decaisnina sumbawensis* (Tiegh.) Barlow

Decaisnina sumbawensis (Tiegh.) Barlow, *Blumea* 38 (1993) 95. — *Amylothea sumbawensis* Tiegh., Bull. Soc. Bot. France 41 (1894) 265. — Type: *Zollinger 3425*, Sumbawa.

Loranthus boholensis Merr., Philipp. J. Sc., Bot. 4 (1909) 141. — *Amylothea boholensis* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 300. — Type: *McGregor BS 1277*, Bohol.

Loranthus formicarium Elmer, Leaflet Philipp. Bot. 3 (1911) 1069. — *Amylothea formicaria* (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 301. — Type: *Elmer 11304*, Mindanao.

Loranthus agusanensis Elmer, Leaflet Philipp. Bot. 6 (1913) 1962. — *Amylothea agusanensis* (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 300. — Type: *Elmer 13405*, Mindanao.

Loranthus terminaliflorus Elmer, Leaflet Philipp. Bot. 6 (1913) 1970. — Type: *Elmer 14156*, Mindanao.

Amylothea parvifolia Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 248. — *Decaisnina parvifolia* (Danser) Barlow, Austral. J. Bot. 22 (1974) 541. — Type: *Mayr 51*, Irian Jaya, Arfak Mts.

Glabrous except for the inflorescence rarely sparsely pubescent. *Leaves* opposite; lamina narrowly elliptic or ovate to broadly ovate, mostly 5–14 cm long, mostly 2–6 cm wide, cuneate to truncate at the base to a petiole 2–12 mm long, usually acuminate and acute to obtuse at the apex, shining and often varnished above, dull below; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes, a raceme of 4–6 opposite evenly spaced pairs of triads with the central flower sessile and the lateral flowers sessile or very shortly pedicellate; axis usually 20–40 mm long, flowerless in the lower 4–15 mm; peduncles of the triads 1.5–3 mm long, secund; pedicels of the lateral flowers (when present) up to 0.5 mm long. *Corolla* in mature bud 6-merous, 22–30 mm long, weakly inflated at the base, slender above, acute at the apex, mostly red below and green or yellow above; petals in the open flower coherent in the lower 1–3 mm. *Anther* 2–3 mm long, acute, usually slightly shorter than the free part of the filament. — **Fig. 19.**

Distribution — Eastern *Malesia*, from the Philippines, Celebes and Lesser Sunda Islands to western New Guinea.

Habitat & Ecology — Humid forests and agricultural lands, 0–2400 m altitude; recorded hosts include *Citrus*, *Coffea*, *Ficus*, and *Nothofagus*.

Note — The species is circumscribed broadly, including taxa such as *Amylothea boholensis*, *A. formicaria* and *A. parvifolia* treated as distinct species by Danser; for discussion see Barlow, *Blumea* 38 (1993) 96.



Fig. 19. *Decaisnina sumbawensis* (Tiegh.) Barlow. Flores. Photo E. Schmutz, 1974, with permission.

19. *Decaisnina triflora* (Span.) Tiegh.

Decaisnina triflora (Span.) Tiegh., Bull. Soc. Bot. France 42 (1895) 436; Barlow, Austral. J. Bot. 22 (1974) 544; in Handb. Fl. Papua New Guinea 2 (1981) 239. — *Loranthus triflorus* Span., Linnaea 15 (1841) 208. — *Amylothea triflora* (Span.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 302; 11 (1931) 250; Blumea 3 (1938) 38, excl. var. *pedicellata* Danser [= *Decaisnina pedicellata* (Danser) Barlow]. — Type: *Spanoghe s.n.*, Timor.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 250; Barlow, Austral. J. Bot. 22 (1974) 544; Blumea 38 (1993) 97].

Glabrous except for the inflorescence axis rarely sparsely tomentose. *Leaves* opposite; lamina narrowly to broadly elliptic, 6–12 by mostly 3–6 cm, attenuate to cuneate at the base to a petiole mostly 4–15 mm long, rounded at the apex, relatively thick, dull and sometimes glaucous on both sides, sometimes slightly darker above; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes, a raceme of 4–9 opposite evenly spaced pairs of triads with all flowers sessile; axis mostly 30–40 mm long; peduncles of the triads 3–6 mm long, secund. *Corolla* in mature bud 6-merous, 20–35 mm long, sometimes very slightly inflated at the base, slender to moderately robust, acute or obtuse at the apex, mostly red but variously orange or yellow or green, often yellow or green above; petals in the open flower coherent in the lower 1–4 mm. *Anther* 1.5–3 mm long, acute, equal to or shorter than the free part of the filament.

Distribution — Northern Australia; *Malesia*: Lesser Sunda Islands, Moluccas, New Guinea.

Habitat & Ecology — Closed and open humid and seasonal forests, 0–2300 m altitude, only reaching the higher altitudes in New Guinea; recorded hosts include *Acacia*, *Alphitonia*, *Barringtonia*, *Buchanania*, *Castanopsis*, *Dillenia*, *Elaeocarpus*, *Engelhardtia*, *Ervatamia*, *Ficus*, *Glochidion*, *Lithocarpus*, *Neoscortechinia*, and an unidentified species of *Euphorbiaceae*.

Note — For circumscription as a species see Barlow, Blumea 38 (1993) 98.

20. *Decaisnina viridis* (Merr.) Barlow

Decaisnina viridis (Merr.) Barlow, Blumea 38 (1993) 99. — *Loranthus viridis* Merr., Philipp. J. Sc. 1, Suppl. (1906) 189. — *Amylothea viridis* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 303. — Type: *Borden FB 816*, lecto, Luzon, Mt Mariveles.

[For additional synonymy see Barlow, Blumea 38 (1993) 99].

Glabrous. *Leaves* opposite or rarely ternate; lamina lanceolate to elliptic, 6–12 by 2.5–6 cm, cuneate at the base to a petiole 10–35 mm long, shortly attenuate to acuminate and acute to rounded at the apex, glossy above, dull brown below; venation pinnate with the midrib distinct above and raised below and the laterals indistinct. *Inflorescences* at the nodes and apparently sometimes terminal, a raceme of 2 or 3 opposite usually subcapitate pairs of triads with the central flower sessile and the lateral flowers pedicellate; axis 17–50 mm long, subtended at the base by an involucre of short thick triangular erect bracts, thick and dilated upwards; peduncles of the triads 7–17 mm long, thick,

not secund; pedicels of the lateral flowers 3–8 mm long, thick. *Corolla* in mature bud 6-merous, 30–47 mm long, robust, inflated to more than 5 mm wide in the basal part, clavate and obtuse at the apex, yellow or green; petals in the open flower coherent in the lower 2.5–10 mm. *Anther* 6–8 mm long, obtuse, 1.2–2 times as long as the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — Gallery forests, 0–1650 m altitude; no hosts recorded.

Note — For distinction as a species and taxonomic position see Barlow, *Blumea* 38 (1993) 99.

21. *Decaisnina zollingeri* (Tiegh.) Barlow

Decaisnina zollingeri (Tiegh.) Barlow, *Blumea* 38 (1993) 100. — *Amylothea zollingeri* Tiegh., Bull. Soc. Bot. France 41 (1894) 264. — Type: *Zollinger s.n.*, Celebes.
[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 252].

Glabrous. Stem internodes when young flattened towards the apex and 4-ridged, 2 ridges forming sharp edges and 2 forming crests on the flattened faces, terete when older. *Leaves* opposite or slightly displaced; lamina oblong to ovate, 4–8(–13) by 2–5.5 (–7.5) cm, truncate or shortly cuneate at the base to a petiole 2–4(–10) mm long, attenuate or acuminate and acute or obtuse at the apex, thin when dry, dull on both sides, sometimes slightly darker above; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes, a raceme of 3–8 opposite evenly spaced pairs of triads with the central flower sessile and the lateral flowers sessile or very shortly pedicellate; axis 25–50 mm long, lacking triads in the lower 10–20 mm; peduncles of the triads 1–2 mm long, secund. *Corolla* in mature bud 6-merous, 20–27 mm long, inflated at the base, slender in the middle, weakly clavate and obtuse at the apex, green or yellow, sometimes with red in the basal part; petals in the open flower separating to the inflated basal part. *Anther* 3–4 mm long, acute, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Java (Kangean Archipelago), Celebes, Lesser Sunda Islands (Alor), Moluccas, western New Guinea.

Habitat & Ecology — 0–620 m altitude; the only recorded host is *Albizia*.

Notes — 1. Closely related to *Decaisnina stenopetala*, *D. sumbawaensis* and possibly *D. cumingii*; for distinction as a species see Barlow, *Blumea* 38 (1993) 101.

2. The inflation of the corolla base may be transient at anthesis, and not consistently visible.

DENDROPTHOE

Dendrophthoe Mart., *Flora* 1 (1830) 109; Tiegh., Bull. Soc. Bot. France 42 (1895) 241; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 397. — Type species: *Dendrophthoe farinosus* (Desr.) Mart. [= *Dendrophthoe pentandra* (L.) Miq.].
[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 397].

Aerial stem-parasitic shrubs, often robust, usually with epicortical runners bearing secondary haustoria. *Leaves* commonly alternate or scattered, less commonly opposite. *Inflorescence* a simple raceme or spike, sometimes very few-flowered and seemingly umbellate; bract single under each flower, simple. *Corolla* 5- or rarely 4-merous, gamopetalous, usually weakly zygomorphic but sometimes regular. *Anthers* basifixed, immobile. *Style* simple, usually with a knob-like stigma. *Fruit* ovoid. — **Fig. 2, 20–23.**

Distribution — About 38 species in tropical Africa, southern Asia and southeastwards to Australia. In *Malesia* 21 species, without an obvious centre of diversity.

Habitat — Humid and open forests, more common in lowlands but some species reach altitudes above 2600 m.

Ecology — In Malesia many species are aggressive, with broad host ranges, often occurring on cultivated trees.

Phylogeny & Biogeography — *Dendrophthoe* displays several characters which may be plesiomorphic for Afro-Asian *Loranthaceae*. The genus is probably a relatively unspecialized derivative of a Gondwanan stock which reached Asia after fragmentation of Gondwana; for further discussion see Barlow in Baas et al. (eds.), *The plant diversity of Malesia* (1990) 273–292. Several more specialized Asian genera with $x = 9$ and relatively small chromosomes are probably derived in situ from a *Dendrophthoe*-like ancestral stock.

KEY TO THE SPECIES

- 1a. Anthers finely acuminate and acute 2
- b. Anthers blunt, sometimes broadly acute but not acuminate 5
- 2a. Corolla 55–90 mm long **12. *D. longituba***
- b. Corolla 18–55 mm long 3
- 3a. Bracts longer than the ovary; flowers closely sessile; inflorescence and flowers with a dense long loose indumentum **10. *D. lanosa***
- b. Bracts shorter than the ovary; flowers shortly pedicellate; inflorescence and flowers with a close tomentum or glabrescent 4
- 4a. Indumentum ochre to red-brown; stems robust; lamina 10–25 cm long; corolla less than 30 mm long **2. *D. constricta***
- b. Indumentum white to light ochre; stems slender; lamina mostly 5–10 cm long; corolla usually more than 30 mm long **1. *D. clementis***
- 5a. Inflorescence axis normally more than 40 mm long and bearing more than 20 flowers 6
- b. Inflorescence axis up to 30 mm long and bearing up to 20 flowers 10
- 6a. Corolla less than 50 mm long 7
- b. Corolla more than 50 mm long 9
- 7a. Inflorescence and flowers entirely glabrous; corolla mostly more than 30 mm long **7. *D. glabrescens***
- b. Inflorescence and flowers sparsely to densely ochre- to red-brown-tomentose; corolla mostly less than 30 mm long 8

- 8a. Leaves thickly coriaceous, bullate between the depressed midrib and lateral veins; anther much shorter than the free part of the filament; corolla split to near the middle at anthesis **4. *D. flosculosa***
- b. Leaves thinly coriaceous, not bullate; veins not depressed; anther \pm equal to the free part of the filament; corolla split almost to the base at anthesis **19. *D. x rimituba***
- 9a. Corolla densely tomentose, lacking knobs on the petals; leaf lamina relatively thin **9. *D. incarnata***
- b. Corolla in mature bud glabrous or nearly so, with a knob on each petal just below the neck; leaf lamina relatively thick **17. *D. praelonga***
- 10a. Corolla tube regular, inflated and more or less bell-shaped. 11
- b. Corolla tube more or less curved, slender or weakly inflated, gradually widened upwards, usually split more deeply on one side 13
- 11a. Leaves linear to narrow lanceolate, pendulous; corolla 4-merous, in mature bud not winged or longitudinally ribbed in the inflated part; inflorescence a false umbel of 2 or 3 flowers of almost equal age **20. *D. timorana***
- b. Leaves elliptic to ovate or obovate, spreading; corolla 5- or rarely 4-merous, in mature bud winged or longitudinally ribbed in the inflated part; inflorescence a few- to several-flowered raceme, sometimes subumbellate 12
- 12a. Corolla glabrous or nearly so; fruit warty; inflorescence 2- to 4-flowered **15. *D. pauciflora***
- b. Corolla sparsely to densely white or grey (rarely brown) tomentose; fruit smooth; inflorescence usually 6- to 12-flowered **16. *D. pentandra***
- 13a. Inflorescences several, clustered at enlarged gall-like leafless nodes 14
- b. Inflorescences solitary or few, in leaf axils or at younger leafless nodes 15
- 14a. Leaves thin, undulate at margin when dry, with slender petiole **5. *D. gangliiformis***
- b. Leaves thick, not undulate at margin when dry, with a thick winged petiole **11. *D. locellata***
- 15a. Corolla less than 20 mm long **6. *D. gjellerupii***
- b. Corolla 20–30 mm long 16
- c. Corolla more than 30 mm long 18
- 16a. Inflorescence and flowers with a persistent thick red-brown indumentum; corolla in mature bud more or less cylindric **21. *D. trichanthera***
- b. Inflorescence and flowers with a short tomentum, the corolla glabrescent; corolla in mature bud with a distinct neck 17
- 17a. Corolla 4-merous, obtuse in mature bud **18. *D. quadrifida***
- b. Corolla 5-merous, attenuate towards an acute apex in mature bud **13. *D. mearnsii***
- 18a. Leaves opposite, sessile, cordate at the base **8. *D. hallieri***
- b. Leaves mostly scattered, petiolate, not cordate at the base 19
- 19a. Leaves usually darker and more lustrous on the upper surface . . . **3. *D. curvata***
- b. Leaves dull on both sides 20
- 20a. Inflorescence entirely glabrous; calyx limb truncate **7. *D. glabrescens***
- b. Inflorescence and flowers white tomentose, especially the ovary; calyx limb distinctly toothed **14. *D. odontocalyx***

1. *Dendrophthoe clementis* (Merr.) Danser

Dendrophthoe clementis (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 307. — *Loranthus clementis* Merr., Philipp. J. Sc. 1, Suppl. (1906) 186. — Type: *Clemens s.n.*, Mindanao, Lake Lanao. [For additional synonymy see Danser, Philipp. J. Sc. 58 (1935) 112, excluding *Dendrophthoe (Loranthus) hallieri*].

Glabrous except for the ovary with a white or light ochre tomentum and the young parts tomentose but soon glabrescent. *Leaves* scattered; lamina narrowly elliptic to rhomboid, 5–10(–15) by 3–7 cm, cuneate to attenuate at the base to a petiole 5–15 mm long, sometimes attenuate and finally broadly acute to shortly rounded at the apex, dull on both sides; venation pinnate and somewhat curvinerved, the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes or rarely terminal on leafy branches, a (20–)30–50-flowered raceme; axis 15–55 mm long; pedicels mostly 1–3 mm long. *Corolla* in mature bud 5-merous, (25–)32–45 mm long, very slender, weakly clavate and acute at the apex, red or yellow, sometimes one colour below and the other above; tube in the open flower 20–30 mm long with the lobes reflexed or twisted slightly higher. *Anther* 2–3 mm long, acute, about half as long as the free part of the filament.

Distribution — *Malesia*: Borneo, Philippines.

Habitat & Ecology — 0–1500 m altitude; no hosts recorded.

Note — Closely related to *Dendrophthoe constricta* from Borneo and Celebes, differing in less robust habit, usually smaller leaves, paler indumentum, longer flowers and glabrous corolla.

2. *Dendrophthoe constricta* (Korth.) Danser

Dendrophthoe constricta (Korth.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 307; 11 (1931) 400. — *Loranthus constrictus* Korth., Verh. Bat. Genootsch. 17 (1839) 276. — Type: *Korthals s.n.*, Borneo, Mantalet River.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 400].

Glabrous except for young shoots, inflorescences and flowers ochre to red-brown stellate hairy, eventually glabrescent except for the ovary. *Leaves* scattered; lamina ovate or elliptic, (7–)10–25 by (3–)5–14 cm, cuneate to truncate at the base to a petiole 5–10 mm long, mostly obtuse or rounded or sometimes acute at the apex, dull on both sides; venation pinnate with the midrib and the somewhat curvinerved main laterals distinct above and prominent and raised below. *Inflorescences* at the nodes, a 10- to 20-flowered raceme; axis 10–20(–40) mm long; pedicels 0.5–1 mm long. *Corolla* in mature bud 5-merous, (18–)22–26(–30) mm long, slender, weakly clavate and acute at the apex, mostly cream or yellow or green below and red above; tube in the open flower 14–20 mm long with the lobes reflexed 2–4 mm higher, slightly curved. *Anther* 1–1.5 mm long, acute, half to one fourth as long as the free part of the filament.

Distribution — *Malesia*: Borneo, Celebes.

Habitat & Ecology — 0–2300 m altitude; recorded hosts include *Citrus*, *Dysoxylum*, *Erythroxylon*, *Ficus*, *Gnetum*, *Melastoma*, *Myristicaceae*, *Nephelium*, *Saurauia*, *Shorea*, and *Villebrunnea*.

Note — Occasional specimens with pale indumentum or an apparently slender habit show transition to *Dendrophthoe clementis*.

3. *Dendrophthoe curvata* (Blume) Miq.

Dendrophthoe curvata (Blume) Miq., Fl. Ind. Bat. 1, 1 (1856) 820; Tiegh., Bull. Soc. Bot. France 42 (1895) 252; Barlow, Blumea 40 (1995) 17. — *Loranthus curvatus* Blume, Bijdr. (1826) 665. — Type: *Blume s.n.*, Java, Mt Salak.

Loranthus falcatus auct. non L. f., Suppl. Pl. (1781) 211. — *Dendrophthoe falcata* auct. non (L. f.) Ettingsh., Denkschr. K. Akad. Wiss., Math.-Nat. Kl. Wien 32 (1872) 52; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 403; Backer & Bakh. f., Fl. Java 2 (1965) 73; Barlow, Austral. J. Bot. 22 (1974) 607; in Handb. Fl. Papua New Guinea 2 (1981) 240.

[For additional synonymy see Barlow, Blumea 40 (1995) 17].

Glabrous except for the young parts, inflorescence, ovary and usually the corolla white- to red-brown-tomentose, the leaves usually soon glabrescent; very rarely completely glabrous. *Leaves* scattered or subopposite; lamina narrowly to broadly ovate or obovate, (4–)10–15 by (1.5–)3–5(–8) cm, attenuate to cuneate at the base to a petiole usually 10–20 mm long, mostly obtuse or rounded (sometimes acute) at the apex, darker and glossy above or dull on both sides; venation pinnate with the midrib and the main laterals visible above and often more distinct below. *Inflorescences* at the nodes, a (2–) 5–10(–16)-flowered raceme; axis 10–25(–30) mm long; pedicels (1–)2–4(–5) mm long. *Corolla* in mature bud 5-merous, (28–)30–48 mm long, uniformly widened upwards, slightly narrowed to a neck and usually weakly clavate and acute at the apex, various shades of yellow to red and often differently coloured below and above; tube in the open flower 18–30 mm long with the lobes reflexed 4–6 mm higher, curved, more deeply split on one side. *Anther* 3–5 mm long, obtuse, 0.5–1 times as long as the free part of the filament. — **Fig. 23e.**

Distribution — Northern Australia, Solomon Islands; *Malesia*: widespread from Sumatra to New Guinea but absent from Philippines and Lesser Sunda Islands.

Habitat & Ecology — Predominantly in humid forests, common in lowlands, frequent up to 2000 m altitude, reaching 3000 m in Sumatra in specimens transitional to *Dendrophthoe × rimituba*; recorded hosts in Malesia include many genera from many different families.

Notes — 1. The species appears to be represented in Sumatra mostly by forms which are transitional to *Dendrophthoe × rimituba*. In Borneo transitional forms to *D. pentandra* are common (see note there).

2. The species has until recently been subsumed in *Dendrophthoe falcata*, which was regarded as a very polymorphic species extending from India to Australia. For the distinction of *D. curvata* as a species see Barlow, Blumea 40 (1995) 17–20.

4. *Dendrophthoe flosculosa* Danser

Dendrophthoe flosculosa Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 408. — Type: *Docters van Leeuwen* 3989, Sumatra, Fort de Kock (lecto L, here chosen from several syntypes cited by Danser).

Glabrous except for young shoots, inflorescences and flowers ochre to red-brown stellate hairy, eventually glabrescent except for the ovary. *Leaves* opposite or scattered; lamina narrow ovate to ovate, 8–21 by 3–9 cm, truncate at the base to a petiole 3–6(–10) mm long, acuminate and acute at the apex, somewhat lustrous above, dull below; venation pinnate with the midrib prominent and raised below and the midrib and main laterals distinct and depressed above with the lamina bullate between them. *Inflorescences* at the nodes, a (25–)30–60-flowered raceme; axis 15–80 mm long; pedicels 1.5–2.5 mm long. *Corolla* in mature bud 5-merous, 23–26 mm long, slender, weakly clavate and obtuse at the apex, red or orange, sometimes green above; tube in the open flower 16–19 mm long with the lobes reflexed 2–3 mm higher, curved. *Anther* c. 1.5 mm long, obtuse, about one third as long as the free part of the filament.

Distribution — *Malesia*: Sumatra.

Habitat & Ecology — 0–1550 m altitude; the only recorded host is *Citrus*.

Note — Danser circumscribed *Dendrophthoe flosculosa* more widely. Some specimens referred to *D. flosculosa* by Danser, including some syntypes, have been included in *D. × rimituba*. The lectotype is chosen in accordance with the more narrow circumscription of *D. flosculosa*. For distinction as a species, see Barlow, Blumea 40 (1995) 21–23.

5. *Dendrophthoe gangliiformis* Barlow

Dendrophthoe gangliiformis Barlow, Blumea 40 (1995) 21. — Type: Jaag 1304, Alor.

Glabrous except for young shoots, inflorescences and flowers shortly ochre to red-brown tomentose, the leaves and corollas soon glabrescent. *Leaves* scattered; lamina narrowly to broadly ovate, 6–16 by 3.5–7 cm, thin, cuneate at the base to a petiole 3–8 mm long, undulate at the margin, rounded or sometimes broadly obtuse at the apex, dull on both sides; venation pinnate with the midrib and the semicurvinerved main laterals prominent on both sides. *Inflorescences* many at the nodes, arising from cushion-like swellings, a short 4–10-flowered raceme; axis very slender, 12–20 mm long; pedicels 0.5–4 mm long. *Corolla* in mature bud 5-merous, 21–30 mm long, very slender, slightly widened upwards, narrowed to a neck, clavate and acute at the apex; tube in the open flower 14–20 mm long with the lobes reflexed 3–5 mm higher, curved. *Anther* 2–2.5 mm long, obtuse, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Celebes, Lesser Sunda Islands (Alor), Moluccas (Tanimbar).

Habitat & Ecology — 0–800 m altitude; the only recorded host is *Ficus*.

6. *Dendrophthoe gjellerupii* (Lauterb.) Danser

Dendrophthoe gjellerupii (Lauterb.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 309; 11 (1931) 409; Barlow, Austral. J. Bot. 22 (1974) 608; in Handb. Fl. Papua New Guinea 2 (1981) 242. — *Loranthus gjellerupii* Lauterb., Nova Guinea 8 (1912) 815. — Type: *Gjellerup* 143, Irian Jaya, 'Hollandia' (= Jayapura).

Glabrous except for the young shoots, inflorescences and flowers off-white to brown tomentose, the leaves soon glabrescent. *Leaves* opposite or scattered; lamina elliptic, 5–9 by 2.5–4 cm, cuneate or attenuate at the base to a petiole 8–12 mm long, obtuse or rounded at the apex, dull on both sides but darker above; venation pinnate with the midrib and the main laterals visible above and distinct below. *Inflorescences* at the nodes, a 4–8-flowered raceme; axis 6–16 mm long; pedicels (0–)1–2.5 mm long. *Corolla* in mature bud 5-merous, 12–16 mm long, slender, gradually widened upwards, constricted just below the apex, shortly clavate and rounded or truncate at the apex, yellow to red; tube in the open flower 8–10 mm long with the lobes reflexed 1–3 mm higher, curved. *Anther* c. 1 mm long, obtuse, about half as long as the free part of the filament.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — 0–460 m altitude; recorded hosts include *Diospyros* and *Timonius*.

7. *Dendrophthoe glabrescens* (Blakely) Barlow

Dendrophthoe glabrescens (Blakely) Barlow, Proc. Linn. Soc. New S Wales 87 (1962) 55. — *Loranthus vitellinus* var. *glabrescens* Blakely, Proc. Linn. Soc. New S Wales 50 (1925) 19. — Type: *Maiden s.n.*, Australia, Rockhampton.

Dendrophthoe pelagica Barlow, Austral. J. Bot. 22 (1974) 609; in Handb. Fl. Papua New Guinea 2 (1981) 242. — Type: *Brass* 6330, New Guinea, Daru I.

[For additional synonymy see Barlow in Fl. Austral. 22 (1984) 125].

Glabrous. *Leaves* scattered or subopposite; lamina narrow lanceolate to elliptic or obovate, 5–8(–20) by 1.5–4 cm, attenuate at the base to a petiole (3–)8–25 mm long, rounded at the apex, dull on both sides; venation pinnate with the midrib distinct and the main laterals usually visible on both sides. *Inflorescences* at the nodes, a (3–)5–10(–20)-flowered raceme; axis (5–)30–60 mm long; pedicels 3–6 mm long. *Corolla* in mature bud 5-merous, 30–45(–50) mm long, uniformly widened upwards, slightly narrowed to a neck, cylindrical or weakly clavate and acute at the apex, mostly yellow, often darkening with age, sometimes red especially in the upper part; tube in the open flower 20–35 mm long with the lobes reflexed 2–4 mm higher, curved. *Anther* 3–5 mm long, obtuse, 0.5–1 times as long as the free part of the filament.

Distribution — Australia; *Malesia*: Lesser Sunda Islands (Lombok, Timor, Alor), Papua New Guinea (Western Province).

Habitat & Ecology — Monsoon forests and woodlands, 0–1200 m altitude; recorded hosts in *Malesia* include *Eucalyptus*, *Melaleuca*, and *Rhizophora*.

Note — The species tends to geographically replace *Dendrophthoe curvata*, which mostly occurs in humid forests. At the interface between humid forests and seasonal monsoon vegetation in New Guinea and northern Australia there is a morphological transition which indicates there is introgression between the two species.

8. *Dendrophthoe hallieri* (Merr.) Danser

Dendrophthoe hallieri (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 309. — *Loranthus hallieri* Merr., Philipp. J. Sc., Bot. 4 (1909) 140. — Type: *Hallier* 628, Mindanao, Zamboanga.

Glabrous except for the young shoots, inflorescences and flowers shortly ochrous tomentose and soon glabrescent except for the ovary. *Leaves* opposite, sessile; lamina broadly ovate, 5–10 by 3–5.5 cm, cordate at the base, rounded at the apex, dull on both sides; venation pinnate but almost curvinerved with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes, a 3- to 5-flowered raceme; axis 2–8 mm long; the pedicels c. 2 long. *Corolla* in mature bud 5-merous, 30–35 mm long, slender, slightly inflated in the middle, weakly clavate and acute at the apex; tube in the open flower 14–17 mm long with the lobes reflexed 3–5 mm higher, curved. *Anther* c. 3 mm long, obtuse, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Philippines.

Habitat & Ecology — Low altitude; no hosts recorded.

9. *Dendrophthoe incarnata* (Jack) Miq.

Dendrophthoe incarnata (Jack) Miq., Fl. Ind. Bat. 1, 1 (1856) 821. — *Loranthus incarnatus* Jack in Roxb., Fl. Ind., ed. 1, 2 (1824) 213. — Type: *Jack s.n.*, Sumatra, Nias I.

Loranthus leucostachys Molk. in Miq., Pl. Jungh. (1852) 114. — *Dendrophthoe leucostachys* (Molk.) Miq., Fl. Ind. Bat. 1, 1 (1856) 819. — Type: *Junghuhn s.n.*, Sumatra, Tobing.

Dendrophthoe costulata Miq., Sumatra (1860) 138, 344. — Type: *Teijsmann 1082*, Sumatra, Singkarak.

Loranthus grandifrons King, J. As. Soc. Beng. 56, ii (1887) 93. — *Dendrophthoe grandifrons* (King) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 309. — Syntypes: *King's Collector (Kunstler) 786, 2067, Scortechini 926*, all Peninsular Malaysia.

Dendrophthoe villosa Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 425. — Type: *Saimoendt 959*, Sumatra, Batang S Manau.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 411].

Glabrous except for the young shoots, inflorescences and flowers with a short dense white or ochrous stellate tomentum which persists on the ovary, corolla and stamen filaments, otherwise eventually glabrescent. *Leaves* scattered or subopposite; lamina narrowly to broadly ovate, 10–30 by (2–)4–16 cm, shortly attenuate to truncate or slightly cordate at the base to a petiole (7–)10–30 mm long, thin, acuminate and acute or obtuse at the apex, darker and somewhat glossy above or dull on both sides; venation pinnate with the midrib and the incurved main laterals distinct on both sides and more prominent below. *Inflorescences* at the nodes, a 12–40-flowered raceme; axis 50–85 mm long; pedicels 0.3–4 mm long. *Corolla* in mature bud 5-merous, (40–)50–110 mm long, relatively slender, sometimes distinctly narrowed above a globosely or ellipsoidally inflated base, gradually widened upwards, weakly clavate and acute at the apex, mostly pink or red below and green above; tube in the open flower 40–85 mm long, more deeply slit on one side, with the lobes reflexed 3–8 mm higher, curved. *Anther* 3–7 mm long, obtuse, equal to or slightly longer than the free part of the filament.

Distribution — Thailand; *Malesia*: Sumatra, Peninsular Malaysia.

Habitat & Ecology — Mostly 0–200 m altitude, rarely to 1050 m; recorded hosts include *Citrus*, *Ficus*, and *Nephelium*.

Notes — 1. Sumatran plants usually have shorter more slender corollas with a more distinct nectar chamber than plants from Peninsular Malaysia and Thailand.

2. Some plants from Peninsular Malaysia and Thailand, with relatively short widened corollas, may be intergrades to *Dendrophthoe pentandra*.

10. *Dendrophthoe lanosa* (Korth.) Danser

Dendrophthoe lanosa (Korth.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 309; 11 (1931) 412. — *Loranthus lanosus* Korth., Tijdschr. Nat. Gesch. & Phys. 3 (1836) 191, 192. — Type: *Korthals s.n.*, Sumatra, Mt Malintang.

Loranthus siamensis Kurz, J. As. Soc. Beng. 40, ii (1871) 62. — *Dendrophthoe siamensis* (Kurz) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 311; 16 (1938) 31. — Type from Thailand (Siam), Kanburi, Bukit Kethay.

Loranthus casuarinae Ridl., Trans. Linn. Soc. II, 3 (1893) 342, non Miq. (1844).

Dendrophthoe magna Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 416; Backer & Bakh. f., Fl. Java 2 (1965) 72. — Type: *van Steenis 4648*, Java, Mt Gedeh.

Densely red-brown lanate-hairy on the young vegetative parts, inflorescences and flowers, later glabrescent on the stems and leaf upper surfaces. *Leaves* opposite or scattered; lamina narrowly ovate, mostly 5–16 cm long, mostly 2–5 cm wide, truncate or slightly cordate at the base to a petiole 5–25(–35) mm long, acuminate and broadly acute at the apex, glossy above, dull below; venation pinnate with the midrib and main laterals distinct above and prominent below. *Inflorescences* at the nodes, a 3–10-flowered spike; axis (4–)6–30(–60) mm long; bracts foliaceous, 3–10(–15) mm long, appressed to the ovary. *Corolla* in mature bud 5-merous, 28–55 mm long, globose at the base, uniformly widened above, weakly clavate and obtuse at the apex, mostly pink or red beneath the indumentum; tube in the open flower 15–30 mm long, more deeply split on one side, with the lobes reflexed 6–10 mm higher, curved. *Anther* 3–4 mm long, acute, slightly shorter than the free part of the filament. — **Fig. 23c, d.**

Distribution — Thailand; *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java.

Habitat & Ecology — 0–1800 m altitude; recorded hosts include *Dipterocarpus*, *Quercus*, and *Vatica*.

Note — *Dendrophthoe magna* was based on a plant with a longer inflorescence axis and shorter corolla. Variation in both characters is continuous and without any clear geographic pattern except that plants from Java generally have short corollas.

11. *Dendrophthoe locellata* Danser

Dendrophthoe locellata Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 414. — Type: *Bünnemeijer 1131*, Celebes, Lombasang.

Glabrous except for young vegetative parts coarsely golden hairy and the young flowers tomentose but soon glabrescent except for the ovary. *Leaves* scattered; lamina ovate, 6–16 by 3–8 cm, shortly attenuate at the base to a petiole 4–10 mm long, acute at the apex, dull on both sides; venation pinnate with the midrib and the main laterals distinct above and below. *Inflorescences* many at the nodes, arising from cushion-like swellings, a short 1–6-flowered raceme; axis 1–5 mm long; pedicels 1.5–2 mm long. *Corolla* in mature bud 5-merous, 35–40 mm long, slender, weakly clavate and obtuse at

the apex, red or orange; tube in the open flower 25–28 mm long with lobes reflexed 2–3 mm higher, slightly curved. *Anther* c. 5 mm long, obtuse, transversely septate or not, slightly longer than the free part of the filament. — **Fig. 22d.**

Distribution — *Malesia*: Borneo, Celebes.

Habitat & Ecology — 0–950 m altitude; no hosts recorded.

12. *Dendrophthoe longituba* (Elmer) Danser

Dendrophthoe longituba (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 310. — *Loranthus longitubus* Elmer, Leaflet Philipp. Bot. 6 (1913) 1961. — Type: *Elmer 14043*, Mindanao, Mt Urdaneta.

Glabrous except for young shoots, inflorescences and flowers ochrous- to rusty-tomentose, the indumentum persisting on the inflorescence and ovary and usually on the leaf undersurface. *Leaves* scattered, subopposite or subverticillate; lamina ovate, 9–30 by (3.5–)6–16 cm, truncate to cordate at the base to a slender petiole 15–35 mm long, acuminate and acute at the apex, thin, dull on both sides but darker above; venation pinnate with the midrib and the incurved main laterals distinct above and prominent below. *Inflorescences* at the nodes and sometimes on the epicortical runners, a 10- to 20-flowered raceme (or spike); axis 30–60 mm long; pedicels (0–)0.5–1.5 mm long; bracts narrow, acute, longer than the ovary. *Corolla* in mature bud 5-merous, 65–70 mm long, slender, gradually widened to just above the middle and then finely tapered to the apex, mostly yellow, often with red or green in the basal or apical parts; tube in the open flower 40–45 mm long with the lobes reflexed c. 10 mm higher, slightly curved. *Anther* 5–6 mm long, finely acute, about equal to the free part of the filament. — **Fig. 20.**



Fig. 20. *Dendrophthoe longituba* (Elmer) Danser. Borneo, NW Kalimantan, Bindjai. Photo A. Elsener, 1963.

Distribution — *Malesia*: Borneo, Philippines (Mindanao).

Habitat & Ecology — Mostly 0–900 m altitude, rarely to 1850 m; recorded hosts include *Citrus*, *Dipterocarpus*, *Hevea*, *Sandoricum*, and *Vitex*.

Note — Closely related to *Dendrophthoe incarnata* from Peninsular Malaysia and Sumatra, and to *D. praelonga* from Java, differing from both in more slender flowers with finely acute anthers.

13. *Dendrophthoe mearnsii* (Merr.) Danser

Dendrophthoe mearnsii (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 310. — *Loranthus mearnsii* Merr., Philipp. J. Sc., Bot. 2 (1907) 271. — Type: *Merrill 5733*, Mindoro, Mt Halcon.

Glabrous except for young vegetative parts, inflorescences and flowers with a short rusty tomentum, the stems, leaves and corollas glabrescent. *Leaves* scattered; lamina broadly ovate, 5–8 by 3–5.5 cm, shortly attenuate at the base to a petiole 6–10 mm long, rounded at the apex, thin, somewhat undulate at the margin, dull on both sides; venation pinnate with the midrib distinct above and prominent below and the main laterals visible on both sides. *Inflorescences* at the nodes, a c. 5-flowered raceme; axis slender, 6–14 mm long; pedicels 2.5–3.5 mm long. *Corolla* in mature bud 5-merous, 22–24 mm long, slender, slightly inflated and gradually widened upwards, narrowed to a neck, long clavate and acute at the apex, green below and red above; tube in the open flower c. 12 mm long, with the lobes reflexed c. 4 mm higher, nearly straight. *Anther* c. 3.5 mm long, obtuse, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Philippines (Mindoro). Known from type specimen only; possibly rare.

Habitat & Ecology — Recorded at 1800 m altitude; no hosts recorded.

Note — Closely related to *Dendrophthoe curvata*, differing in thinner leaves, dark indumentum and shorter, long-acute corolla buds.

14. *Dendrophthoe odontocalyx* (Benth.) Tiegh.

Dendrophthoe odontocalyx (F. Muell. ex Benth.) Tiegh., Bull. Soc. Bot. France 42 (1895) 87. — *Loranthus odontocalyx* F. Muell. ex Benth., Fl. Austral. 3 (1867) 391. — Type: *Mueller s.n.*, N Australia, between McAdam Range and Providence Hill.

Leucobotrys pilosa Tiegh., Bull. Soc. Bot. France 41 (1894) 545. — *Loranthus pilosus* (Tiegh.) Engl., Nat. Pflanzenfam., Nachtr. 1 (1897) 128. — Type: *Zollinger 3415*, Sumbawa.

[For additional synonymy see Barlow in Fl. Austral. 22 (1984) 126].

Densely white-tomentose on all young parts, eventually glabrescent except for the inflorescence and calyx and sometimes the corolla and leaves. *Leaves* opposite or scattered; lamina narrow lanceolate to elliptic, sometimes falcate, 4–15(–25) by (0.5–)1–4 cm, attenuate or cuneate at the base to a petiole 5–15(–25) mm long, sometimes attenuate and finally obtuse or rounded at the apex, dull on both sides; venation pinnate but in narrow leaves almost curvinerved with the midrib prominent and the main laterals faintly visible on both sides. *Inflorescences* at the nodes, a 3- to 8-flowered raceme; axis 5–25(–40) mm long; pedicels 2–6 mm long. *Corolla* in mature bud 5-merous, 25–42 mm

long, gradually widened upwards, very weakly clavate and acute to rounded at the apex, red, pink, orange or yellow, often more yellowish or greenish above; tube in the open flower 12–25 mm long with the lobes reflexed 4–7 mm higher, curved. *Anther* 5–7 mm long, obtuse, usually slightly longer than the free part of the filament.

Distribution — Australia; *Malesia*: Java (East), Lesser Sunda Islands (Sumbawa, Alor, Timor).

Habitat & Ecology — Monsoon forests and woodlands, 50–900 m altitude; recorded hosts in Malesia include *Eucalyptus*, *Launea*, and *Stadmannia*.

Note — The species tends to geographically replace *Dendrophthoe curvata*, which mostly occurs in humid forests.

15. *Dendrophthoe pauciflora* Danser

Dendrophthoe pauciflora Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 417. — Types: *Riedel s.n.*, lecto, see note 2, Celebes, Gorontalo; *Forsten 455*, syn, Celebes; *Forsten s.n.*, syn, Celebes.

Dendrophthoe mirifica Danser, Philipp. J. Sc. 58 (1935) 115. — Type: *Reillo BS 16160*, Philippines, Basilan.

Glabrous except for young shoots, inflorescences and flowers white to red-brown stellate hairy and sometimes eventually glabrescent. *Leaves* scattered; lamina elliptic to ovate or obovate, 3–11 by 2–6 cm, thin, attenuate or cuneate at the base to a sometimes obscure petiole (1–)3–10 mm long, acute to rounded at the apex, dull on both sides but slightly darker above; venation pinnate but somewhat curvinerved, with the midrib and main laterals raised below and obscure or visible above. *Inflorescences* usually several at the nodes, a 2- to 4-flowered raceme, sometimes subumbellate, sometimes prolonged slightly beyond the flower pedicels; axis (0.75–)2–5 mm long; pedicels 0.75–4 mm long. *Corolla* in mature bud 4- or 5-merous, 11–15(–18) mm long, abruptly inflated 1 mm above the base to 5 mm wide, winged from base to apex, angular towards the apex but finally rounded, yellow below and red above; tube in the open flower 3–4.5(–11) mm long with the lobes reflexed 4 mm higher. *Anther* 1–3 mm long, obtuse, about 0.5–1.5 times as long as the free part of the filament.

Distribution — *Malesia*: Philippines (Basilan), Celebes, Moluccas (Halmahera, Ambon).

Habitat & Ecology — 0–200 m altitude; the only recorded host is *Sesbania*.

Notes — 1. Closely related to *Dendrophthoe pentandra*, which reaches its eastward limits in Borneo and Flores; differs in having thinner leaves, shorter fewer-flowered inflorescence, more campanulate corolla tube and warty fruit.

2. Of the three syntypes cited above, *Riedel s.n.* (BQ) is the most substantial, and is accordingly chosen as lectotype of the species name.

16. *Dendrophthoe pentandra* (L.) Miq.

Dendrophthoe pentandra (L.) Miq., Fl. Ind. Bat. 1, 1 (1856) 818; Backer & Bakh. f., Fl. Java 2 (1965) 72. — *Loranthus pentandrus* L., Mantissa 1 (1767) 63. — Type in LINN.

[For extensive additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 417; 16 (1938) 29].



Fig. 21. *Dendrophthoe pentandra* (L.) Miq. Borneo, W Kalimantan, Wjarumkop. Photo A. Elsener, 1964.

Glabrous except for the young shoots, inflorescences and flowers with a somewhat silky off-white to grey or less often brown tomentum, less dense on the distal part of the corolla. *Leaves* scattered or subopposite; lamina variable, mostly narrowly to broadly elliptic, mostly 6–13 cm long, (1.5–)3–8 cm wide, attenuate to cuneate at the base to a petiole 5–20 mm long, rounded to rarely acuminate and acute at the apex, dull on both sides but darker above; venation pinnate with the midrib and the somewhat curvined main laterals usually visible on both sides. *Inflorescences* at the nodes, a 6–12-flowered raceme; axis 10–20(–35) mm long; pedicels 1–4 mm long. *Corolla* in mature bud 5-merous, 12–20(–28) mm long (longer in some putative hybrids), inflated to c. 5 mm wide and angular or winged in the lower part, narrowed to a neck, clavate and obtuse or rounded at the apex, mostly green or yellow or orange, rarely red; tube in the open flower (2–) 6–12 mm long, narrowly to broadly campanulate, regular, with the lobes reflexed 4–8 mm higher and together often almost closing the neck. *Anther* 2–5 mm long, obtuse, longer or shorter than the free part of the filament. — **Fig. 2, 21, 22 c.**

Distribution — From eastern India eastwards throughout Indochina; *Malesia*: Sumatra, Peninsular Malaysia, Singapore, Borneo, Java, rare in Philippines (Palawan, Luzon) and western Lesser Sunda Islands (Bali, Sumba, Flores).

Habitat & Ecology — Predominantly in humid forests but also in open forests and plantations, common in lowlands up to 500 m altitude, less frequently to 1650 m; recorded hosts many.

Notes — 1. Many intermediate specimens appear to be hybrids, especially with *Dendrophthoe curvata* in Borneo and *D. kerrii* in Indochina.

2. In absence of flowers *Dendrophthoe pentandra* may be difficult to distinguish from *D. curvata*. Typical *D. pentandra* differs from *D. curvata* in being more robust, with stouter stems and thicker darker glabrous leaves; the inflorescence is shorter and fewer-flowered; the corolla always bears a somewhat silky usually off-white indumentum, is inflated in the lower part, has a short regular tube, with the lobes fully reflexed almost closing the neck; the corolla appears to be normally of only one colour, whereas that of *D. curvata* is often differently coloured above and below.

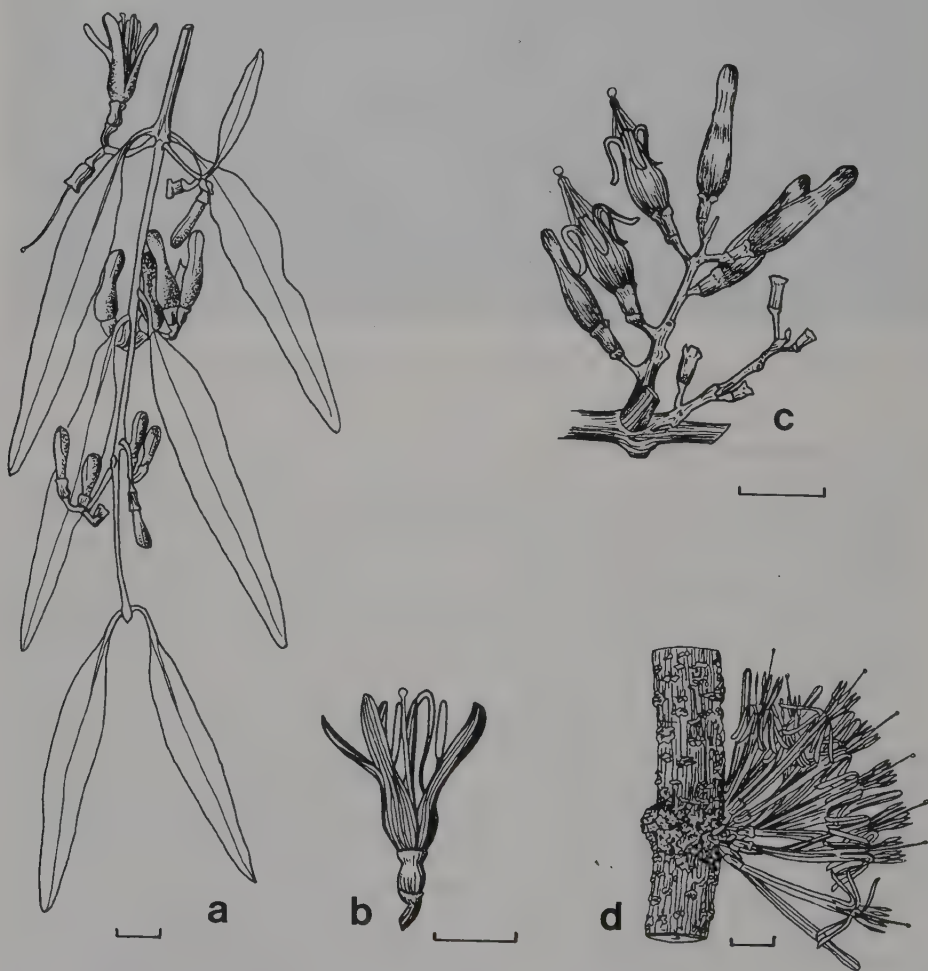


Fig. 22. *Dendrophthoe timorana* (Danser) Barlow. a. Flower-bearing twig; b. flower. — *D. pentandra* (L.) Miq. c. Inflorescence. — *D. locellata* Danser. d. Part of stem with inflorescence (a, b: *Teijsmann s.n.*; c: *Danser s.n.*; d: *Bünnemeijer 11312*). Redrawn from Danser (1931). Scale bars represent 1 cm.

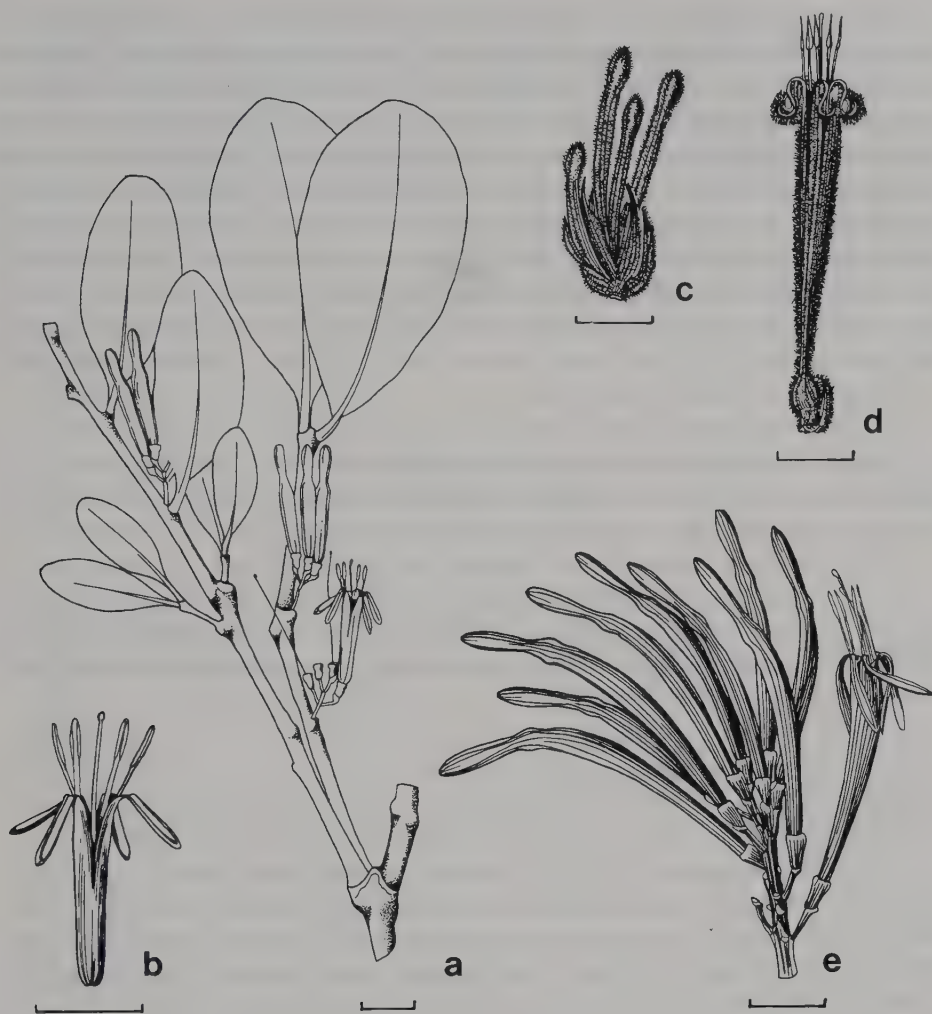


Fig. 23. *Dendrophthoe quadrifida* Danser. a. Flower-bearing twig; b. corolla with stamens and style. — *D. lanosa* (Korth.) Danser. c. Inflorescence with flower buds; d. flower with bract. — *D. curvata* (Blume) Miq. e. Inflorescence (a, b: Clemens 32743; c: Burkill & Haniff 17314; d: Hose 99; e: Backer 9817). a, b Redrawn from Danser (1936), c–e redrawn from Danser (1931). Scale bars represent 1 cm.

17. *Dendrophthoe praelonga* (Blume) Miq.

Dendrophthoe praelonga (Blume) Miq., Fl. Ind. Bat. 1, 1 (1856) 819; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 422; Backer & Bakh. f., Fl. Java 2 (1965) 73. — *Loranthus praelongus* Blume, Bijdr. (1826) 664. — Type: *Blume s. n.*, Java.

Dendrophthoe carinata Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 399; Backer & Bakh. f., Fl. Java 2 (1965) 73. — Type: *Backer 8652*, Java, Mt Cikuray.

Glabrous except for the young shoots, inflorescences and flowers white to pale grey tomentose, soon glabrescent other than the ovary. *Leaves* scattered or rarely opposite; lamina ovate or elliptic, 7–20 by 5–12 cm, thick, cuneate to slightly cordate at the base to a petiole 2–12 mm long, obtuse or rounded at the apex, dull on both sides; venation pinnate with the midrib and the incurved main laterals distinct on both sides and more prominent below. *Inflorescences* at the nodes, a many-flowered raceme; axis 30–60 mm long; pedicels 1–4 mm long. *Corolla* in mature bud 5-merous, (52–)70–110 mm long, gradually widened upwards, thickened on each petal just below the neck, weakly clavate, sometimes angular, truncate or obtuse at the apex, mostly yellow or yellowish green, becoming orange or rarely red with age; tube in the open flower 35–55 mm long with the lobes reflexed 6–10 mm higher, curved. *Anther* 5–9 mm long, obtuse, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Java.

Habitat & Ecology — Common in lowlands from 0 to 1000 m altitude, rarely up to 2300 m; recorded hosts include *Bombax*, *Dalbergia*, *Erythrina*, *Ficus*, *Hevea*, *Hibiscus*, *Lumnitzera*, *Pithecellobium*, *Sonneratia*, and *Swietenia*.

Note — Similar to *Dendrophthoe longituba* from Borneo, differing in thicker leaves less cordate at the base, with shorter petiole; thicker inflorescence axis with flowers more crowded; and robust corolla and obtuse anthers. Also similar to *D. incarnata* of Peninsular Malaysia and Sumatra, differing in thicker leaves; shorter inflorescence axis; and more robust glabrous corolla.

18. *Dendrophthoe quadrifida* Danser

Dendrophthoe quadrifida Danser, Blumea 2 (1936) 39. — Type: *Clemens* 32743, Mt Kinabalu.

Tomentum rusty, persistent on the inflorescence and ovary and sparsely on the corolla, the vegetative parts soon glabrescent. *Leaves* scattered or subopposite; lamina obovate, 2–6 by 1–3 cm, cuneate at the base to a petiole 3–8 mm long, rounded at the apex, dull on both sides but darker above; venation pinnate with the midrib prominent and the main laterals obscure on both sides. *Inflorescences* at the nodes, a 2–6-flowered raceme; axis 5–14 mm long; pedicels 1–3 mm long. *Corolla* in mature bud 4-merous, 26–28 mm long, cylindric below a short neck and clavate and obtuse at the apex, red, sometimes yellow above; tube in the open flower 10–12 mm long with the lobes reflexed 8–10 mm higher, straight. *Anther* c. 4 mm long, obtuse, slightly shorter than the free part of the filament. — **Fig. 23 a, b.**

Distribution — *Malesia*: Borneo (Mt Kinabalu), Moluccas (Halmahera).

Habitat & Ecology — 100–1500 m altitude; no hosts recorded.

19. *Dendrophthoe* × *rimituba* Barlow

Dendrophthoe × *rimituba* Barlow, Blumea 40 (1995) 21. — Type: *Meijer* 3343, Sumatra, Mt Merapi.

Glabrous except for the inflorescence densely and the flowers sparsely to densely red brown tomentose or sometimes the corolla glabrous. *Leaves* opposite or scattered; lami-

na narrowly ovate to ovate, (6–)8–15(–18) by (3–)6–9 cm, truncate to attenuate at the base to a petiole 7–20 mm long, thin, finely undulate at the margin, acuminate and acute at the apex, dull on both sides or darker and slightly lustrous above; venation pinnate with the midrib distinct above and raised below and the main laterals somewhat curvinnerved and usually visible. *Inflorescences* at the nodes, a 15–30-flowered raceme; axis 40–65 mm long; pedicels 1–3.5(–6) mm long. *Corolla* in mature bud 5-merous, 20–26 (–32) mm long, slender, gradually widened upwards, narrowed to a weak neck, abruptly widened and clavate below the rounded or obtuse apex, red; tube in the open flower 15–24 mm long with the lobes reflexed 2–3 mm higher, hardly curved but split almost to the base on one side. *Anther* 1.5–2 mm long, obtuse, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Sumatra.

Habitat & Ecology — 0–1600 m altitude; the only recorded host is coffee.

Note — The species may be a stabilized hybrid derived from *Dendrophthoe flosculosa* and *D. curvata*. For distinction as a species, see Barlow (1995). Many Sumatran specimens appear to be intergrades to *D. curvata*, and are not resolved by the key.

20. *Dendrophthoe timorana* (Danser) Barlow

Dendrophthoe timorana (Danser) Barlow, Blumea 40 (1995) 23. — *Amyema timorana* Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 350. — Type: *Teijsmann s.n.*, Timor.

Glabrous except for the young parts, inflorescences and flowers densely white tomentose. *Leaves* scattered or subopposite, pendulous; lamina linear-lanceolate, 7–15 by 0.6–2.5 cm, attenuate at the base to a slender petiole 5–20 mm long, thin, attenuate and obtuse at the apex, dull on both sides; venation pinnate with only the midrib distinct. *Inflorescences* at the nodes, a 2- or 3-flowered subumbellate raceme; axis 5–12 mm long; the pedicels c. 3 mm long. *Corolla* in mature bud 4-merous, 12–18 mm long, robust, clavate and obtuse at the apex, green beneath the indumentum; tube in the open flower not seen but probably short, regular, with the lobes reflexed near the middle. *Anther* 3–5 mm long, obtuse, about twice as long as the free part of the filament. —

Fig. 22a, b.

Distribution — *Malesia*: Timor.

Habitat & Ecology — Seasonal open forests and woodlands from 0 to 1400 m altitude; recorded hosts include *Casuarina* (commonly) and *Albizia*.

Note — For explanation of transfer of the species from *Amyema* to *Dendrophthoe*, see Barlow, l.c.

21. *Dendrophthoe trichanthera* Barlow

Dendrophthoe trichanthera Barlow, Austral. J. Bot. 22 (1974) 609; in Handb. Fl. Papua New Guinea 2 (1981). — Type: *Brass* 8667, Papua New Guinea, Wassi-Kussa River.

Glabrous except for the inflorescence and flowers and sometimes the leaf undersurface densely rusty stellate hairy. *Leaves* opposite or scattered; lamina ovate, 3–9 by 1.5–

4.5 cm, cuneate or attenuate at the base to a petiole 5–15 mm long, obtuse or shortly rounded at the apex, dull on both sides; venation pinnate with the midrib and the main laterals distinct above and prominent below. *Inflorescences* at the nodes, a 4–6-flowered more or less subumbellate raceme; axis 4–10 mm long; pedicels 3–5 mm long, dilated upwards. *Corolla* in mature bud 5-merous, (20–)25–30 mm long, almost cylindric, weakly clavate and rounded at the apex, the colour obscured by the indumentum; tube in the open flower (13–)15–19 mm long with the lobes reflexed 4–6 mm higher, slightly curved. *Anther* c. 3 mm long, obtuse, slightly shorter than the free part of the filament.

Distribution — *Malesia*: New Guinea (Fly River area).

Habitat & Ecology — Seasonal open and gallery forest, 0–300 m altitude; recorded hosts include *Agonis*, *Halfordia*, *Melaleuca*, and *Terminalia*.

DISTRANTHES

Distrianthes Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 213; 11 (1931) 366. — Type species: *Distrianthes molliflora* (K. Krause) Danser.

[For synonymy see Barlow, Austral. J. Bot. 22 (1974) 598].

Aerial stem-parasitic shrubs, robust, with epicortical runners bearing secondary haustoria. *Leaves* opposite. *Inflorescence* capitate, consisting of two sessile dichasia (triads) at the apex of a common peduncle; central bracts of the triads enlarged and foliaceous, enclosing the flowers and connate at the margins over them during development; bracts subtending the lateral flowers small, narrow. *Corolla* 6-merous, gamopetalous, regular. *Anthers* basifixed, immobile. *Style* simple, with a knob-like stigma. — **Fig. 24.**

Distribution — One species endemic to New Guinea.

Habitat & Ecology — Humid forests, from lowlands to 1100 m altitude. Host specificity is probably low.

Morphology & Taxonomy — The genus is probably a specialized local derivative of the Australian/Papuan stock of which *Amyema* is the core. The 6-flowered capitate involucre inflorescence is probably a parallel development to that of many *Amyema* species formerly referred to *Dicymanthes*, and to the involucre head of *Papuanthes*. In addition to the involucre, the primary distinction from *Amyema* which it shares with *Papuanthes* is the gamopetalous corolla.

Distrianthes molliflora (K. Krause) Danser

Distrianthes molliflora (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 312; 11 (1931) 367; Barlow, Austral. J. Bot. 22 (1974) 598; in Handb. Fl. Papua New Guinea 2 (1981) 243. — *Loranthus molliflorus* K. Krause, Bot. Jahrb. 57 (1922) 488. — Type: *Schlechter 17784*, Papua New Guinea, Kani Mts.

Loranthus spathatus K. Krause, Bot. Jahrb. 57 (1922) 489. — *Distrianthes spathata* (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 312; 11 (1931) 367. — Type: *Schlechter 20136*, Papua New Guinea, Torricelli Mts.

Loranthus lamii K. Krause, Nova Guinea 14 (1923) 104. — *Distrianthes lamii* (K. Krause) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 312; 11 (1931) 366. — Type: *Lam 1407*, Irian Jaya, Doorman R.

Glabrous except for the young shoots, inflorescences and flowers shortly brown tomentose and the ovary and corolla usually clothed with silky hairs up to 2 mm long. *Leaves* opposite; lamina elliptic to ovate, 12–25 by 4–12 cm, cuneate to truncate at the base to a petiole 4–12 mm long, recurved at the margin, usually acuminate and acute at the apex, lustrous above, dull below; venation pinnate with the midrib and main laterals distinct above and prominent below. *Inflorescences* few at the nodes and scattered along the epicortical runners; peduncle c. 2 mm long, dilated upwards, 2–4 mm wide at apex; central bracts ovate, 12–30(–40) mm long, 4–12 mm wide, acute, often with sutures not visible, later separating nearly to the base or splitting irregularly, orange or red; lateral bracts slender, acute, 1–10 mm long. *Corolla* in mature bud 40–65 mm long, slender, very gradually widened upwards, acute at apex, orange to deep red; tube in open flower 12–50 mm long, with petals reflexed and curled 10–16 mm below stigma. *Anther* 3–4 mm long, half to one third as long as the free part of the filament. — **Fig. 24.**

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Humid forests at 130–1100 m altitude; no hosts recorded.

Note — For comment on conspecificity with *Distrianthes lamii* and *D. spathata*, see Barlow (1974).

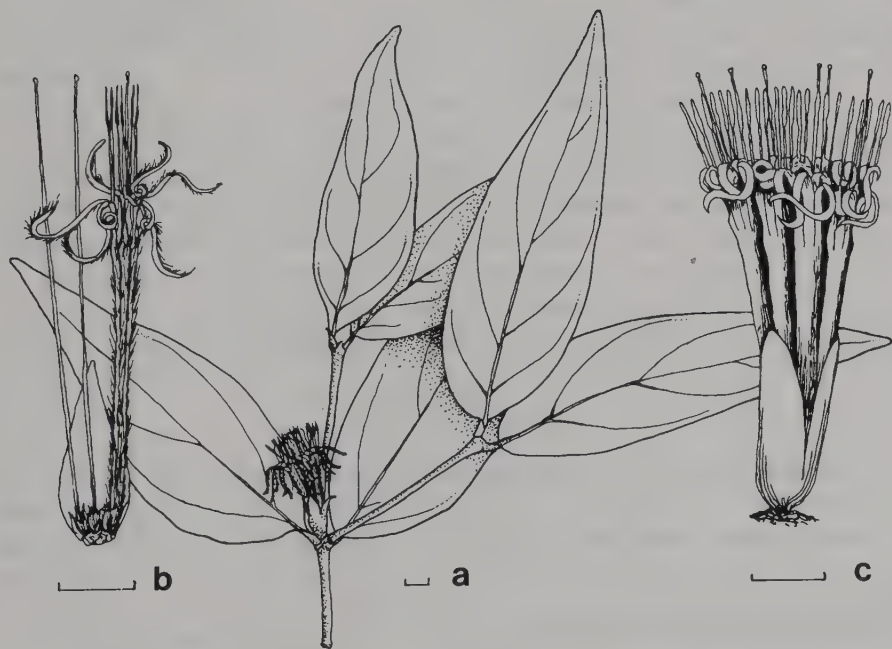


Fig. 24. *Distrianthes molliflora* (K. Krause) Danser. a. Twig with inflorescence; b. inflorescence in sectional view; c. inflorescence (a: not cited; b: *Schlechter 17784*; c: *Lam 1407*). a Redrawn from Barlow (1981), b, c redrawn from Danser (1931). Scale bars represent 1 cm.

ELYTRANTHE

Elytranthe Blume in Schult. & Schult. f., Syst. Veg. 7 (1830) 1611. — Type species: *Elytranthe albida* (Blume) Blume

[For synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 304].

Aerial stem-parasitic shrubs with epicortical runners bearing secondary haustoria. *Leaves* opposite. *Inflorescences* axillary, a few-flowered spike; axis decussately flattened, with the flowers inserted in hollows; bracts 3 under each flower, foliaceous and together enclosing the flower bud. *Corolla* 6-merous, gamopetalous, regular or nearly so. *Anthers* basifixed, immobile. *Style* simple, conical at the base, with a knob-like stigma. *Fruit* almost globular. — **Fig. 25.**

Distribution — Genus of two species distributed from eastern India to Vietnam. In *West Malesia* both species.

Habitat — Mostly open forests, mostly in highlands but extending down to sea level.

Ecology — Plants often robust, forming very large infestations, especially on *Castanea* and *Quercus*.

Morphology & Taxonomy — *Elytranthe* occupies an intermediate position between *Macrosolen*, in which the inflorescence is a simple raceme or spike, and *Lepidaria*, in which it has the same basic structure but is condensed, capitate and involucrate. In *Elytranthe* the spicate inflorescence is still clearly evident, although the bracts are enlarged and closely envelop the developing flowers. However, the inflorescence features of the two species of *Elytranthe* possibly represent parallel developments, so that the genus may not be natural. Danser in Blumea 2 (1936) 35 addressed these problems, but did not find a satisfactory solution. The inflorescence architecture of *Elytranthe albida* and *E. arnottiana* is hardly different from that of the *Macrosolen parasiticus* species group, which Danser had earlier referred to *Elytranthe* but transferred to *Macrosolen* in 1936. The most satisfactory treatment may be to treat *Elytranthe* and *Macrosolen* as congeneric, but confirmation requires a critical study of the inflorescence structure, function and homology. Because the name *Elytranthe* has priority over *Macrosolen*, which is a relatively large genus, union of the two would involve considerable nomenclatural change.

KEY TO THE SPECIES

- 1a. Corolla more than 40 mm long; inflorescence with a peduncle 1–15 mm long **1. *E. albida***
- b. Corolla less than 15 mm long; inflorescence seemingly sessile . . **2. *E. arnottiana***

1. *Elytranthe albida* (Blume) Blume

Elytranthe albida (Blume) Blume in Schult. & Schult. f., Syst. Veg. 7 (1830) 1611; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 305; Backer & Bakh. f., Fl. Java 2 (1965) 70. — *Loranthus albidus* Blume, Verh. Bat. Genootsch. 9 (1823) 184. — Type: *Blume s.n.*, Java.
Loranthus leucosiphon Griff., Not. Pl. As. 4 (1854) 623. — *Elytranthe leucosiphon* (Griff.) Tiegh., Bull. Soc. Bot. France 42 (1895) 439. — Type: *Griffith s.n.*, Malaysia, Malacca.

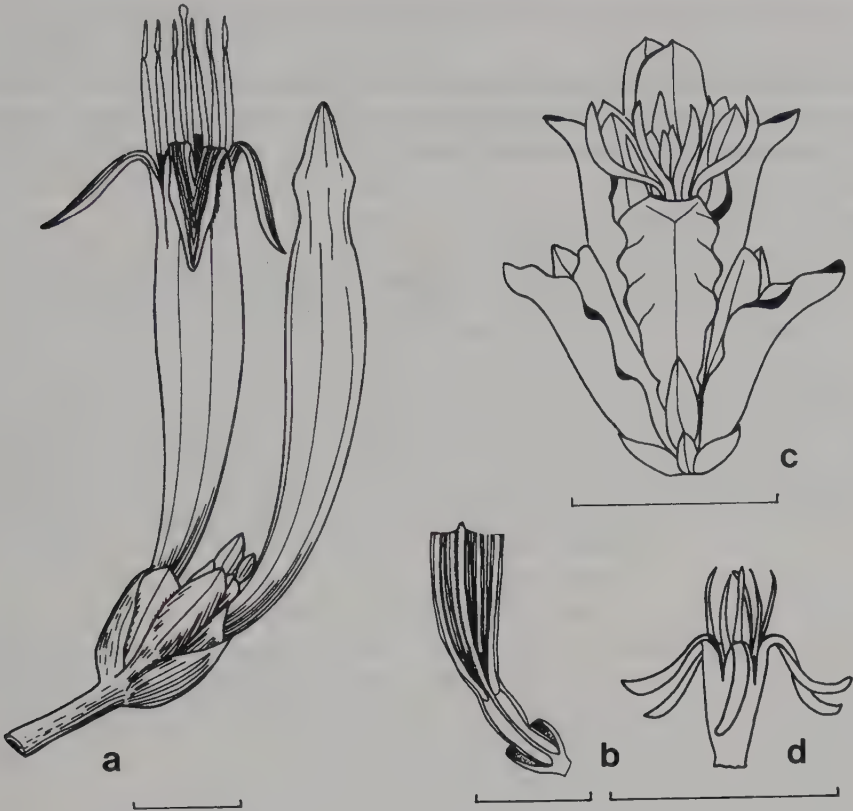


Fig. 25. *Elytranthe albida* (Blume) Blume. a. Inflorescence; b. sectional view of lower part of flower. — *E. arnottiana* (Korth.) Miq. c. Inflorescence; d. corolla and stamens (a, b: Backer 25952; c, d: Burkill 3394). Redrawn from Danser (1931). Scale bars represent 1 cm.

Glabrous. *Leaves* opposite; lamina narrowly to broadly ovate, 6–14 by 3–8 cm, cuneate to truncate at the base to a petiole 7–25 mm long, somewhat acuminate and broadly acute at the apex, dull on both sides; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes, a pedunculate spike of 1–3 decussate pairs of flowers; peduncle (1–)5–10(–15) mm long, more or less terete, subtended by 1–3 pairs of small bracts at the base; flower-bearing axis 5–20 mm long, with decussate hollows c. 6 mm long; central bracts 7–12 by 4–6 mm, keeled, acute; lateral bracts as long as the central ones, keeled, obtuse. *Corolla* in mature bud 6-merous, 40–65 mm long, with a distinct nectar chamber at the base, gradually widened upwards, weakly winged above the middle, narrowed to a neck, clavate and acute at the apex, mostly white to pink below, blue-grey above; tube in the open flower 25–45 mm long, split slightly deeper on one side, with the lobes reflexed or twisted 5–10 mm higher. *Anther* 2.5–3.5 mm long, constricted at the base, acute, about half as long as the free part of the filament. — **Fig. 25a, b.**

Distribution — India to Vietnam; *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java.

Habitat & Ecology — Open and humid forests, commonly from 1000 to 1700 m altitude, less frequently down to sea level; recorded hosts include *Brownlowia*, *Castanopsis*, *Lithocarpus*, *Litsea*, *Shorea*, and *Quercus*.

2. *Elytranthe arnottiana* (Korth.) Miq.

Elytranthe arnottiana (Korth.) Miq., Fl. Ind. Bat. 1, 1 (1856) 832. — *Loranthus arnottianus* Korth., Verh. Bat. Genootsch. 17 (1839) 284. — Type: *Korthals s.n.*, Sumatra, Mt Malingtang. [For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 307].

Glabrous. *Leaves* opposite; lamina ovate to slightly obovate, 5–8 by 3–5 cm, cuneate to truncate at the base to a petiole 4–13 mm long, rounded at the apex, dull on both sides; venation pinnate with the midrib distinct below and the other venation indistinct. *Inflorescences* at the nodes, a spike of 1–3 decussate pairs of flowers, sessile or nearly so, subtended at the base by 1–3 pairs of bracts up to 5 mm long; flower-bearing axis 5–10 mm long, with decussate hollows 3–4 mm long; central bracts c. 10 by 4 mm, sometimes keeled, acute; lateral bracts c. 7 by 2.5 mm wide, obtuse or acute. *Corolla* in mature bud 6-merous, c. 10 mm long, with a weakly defined nectar chamber at the base, gradually widened upwards, slightly narrowed above the middle to a neck, clavate and broadly acute at the apex, green, sometimes orange-tinged below; tube in the open flower c. 6 mm long with the lobes reflexed c. 1 mm higher. *Anther* c. 1.5 mm long, obtuse, about equal to the free part of the filament. — **Fig. 25c, d.**

Distribution — *Malesia*: Sumatra, Peninsular Malaysia, Singapore.

Habitat & Ecology — Probably low altitudes; no hosts recorded.

HELIXANTHERA

Helixanthera Lour., Fl. Coch. 1 (1790) 142; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 368. — Type species: *Helixanthera parasitica* Lour. [For synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 368].

Aerial stem-parasitic shrubs, sometimes with epicortical runners bearing secondary haustoria, or rarely (not in *Malesia*) terrestrial root parasites. *Leaves* opposite, scattered or sometimes crowded to false whorls. *Inflorescence* a simple raceme or spike; bracts single under each flower. *Corolla* 4- to 6-merous, choripetalous, regular or nearly so. *Anthers* basifixed, immobile. *Style* straight, simple or with a constriction separating upper and lower segments with different outlines; stigma knob-like. *Fruit* ovoid. — **Fig. 26, 27.**

Distribution — About 35 species in tropical Africa, southern Asia and *Malesia*. In *Malesia* 11 species with their diversity centred on Peninsular Malaysia, Sumatra and Borneo, and reaching the Philippines, Celebes and Java.

Habitat — Humid and open forests and cultivated lands, commonly from 0 to 1800 m altitude but some species reaching 3000 m.

Ecology — Host specificity is low; some species are aggressive, with broad host ranges, often occurring on cultivated trees.

Morphology — Several groups of species in *Helixanthera* are defined by differences especially in the form of the ovary, corolla and style. The ovary may be of the shortly cylindric or urceolate form typical of the family generally, or greatly elongated. The corolla in bud may be slightly curved, gradually tapered and acute (described as ‘beak-like’ by Danser) or regular; in the latter case it may be campanulate and winged below or not. The style may reach to the top of the flower, as in most loranth, or only to near the base of the anthers; it may be simple or articulate, with lower and upper segments which may differ in width and angularity.

Taxonomy — Combinations of the differences mentioned above have provided the basis for recognition of segregate genera, especially by Van Tieghem. Danser (1929, 1933) considered that there was little to justify the acceptance of a large number of small genera based on these differences, and his view is followed here. However, circumscription of a single diverse genus *Helixanthera* presents some difficulties in distinction of the closely related genus *Loranthus* (see discussion there).

KEY TO THE SPECIES

- 1a. Corolla more than 15 mm long 2
- b. Corolla less than 13 mm long 4
- 2a. Pedicels flattened, winged and widened upwards; corolla 6-merous .. **1. *H. alata***
- b. Pedicels angular but not flattened or winged; corolla 5-merous 3
- 3a. Pedicel shorter than ovary; inflorescence axis 20–60 mm long **3. *H. crassipetala***
- b. Pedicel mostly longer than the ovary; inflorescence axis 50–250 mm long **4. *H. cylindrica***
- 4a. Style reaching to the top of the anthers; inflorescence axis less than 70 and often less than 50 mm long 5
- b. Style reaching only to near the base of the anthers; inflorescence axis more than 60 and often more than 100 mm long 8
- 5a. Flowers sessile; petals commonly 5, sometimes 4 6
- b. Flowers pedicellate, sometimes very shortly; petals 4 7
- 6a. Leaves rounded at the apex; inflorescence axis up to 40 mm long; corolla rounded in bud, 3.5–5 mm long; anther shorter than the free filament **9. *H. sessiliflora***
- b. Leaves acute at the apex; inflorescence axis more than 45 mm long; corolla acute in bud, 5–7 mm long; anther longer than the free filament **6. *H. maxwelliana***
- 7a. Inflorescence of 10–30 flowers distributed along an axis 15–70 mm long; free filament longer than the anther **2. *H. coccinea***
- b. Inflorescence of 2–5 flowers subumbellately crowded near the tip of an axis 5–20 mm long; free filament much shorter than the anther **5. *H. ligustrina***
- 8a. Style angular in the lower part below a constriction near the middle, more slender above. 9
- b. Style terete or angular, gradually widened upwards, lacking a constriction 10

- 9a. Flowers sessile; bracts strongly reflexed, with a dorsal spur-like sac; style weakly constricted **11. *H. spicata***
- b. Flowers pedicellate, sometimes very shortly; bracts not strongly reflexed, sometimes with a dorsal transverse fold but lacking a sac; style strongly constricted ..
..... **7. *H. parasitica***
- 10a. Inflorescence sometimes subtended by an involucre of a few narrow bracts up to 5 mm long; ovary barrel-shaped or shortly cylindric, usually with irregular wrinkles or furrows persisting to the young fruit; corolla 3.5–8.5 mm long
..... **8. *H. pulchra***
- b. Inflorescence subtended by an involucre of numerous linear bracts up to 15 mm long; ovary cylindric, longer than wide, usually slightly narrowed below the calyx limb, sometimes longitudinally weakly angled or furrowed; corolla 7–12 mm long
..... **10. *H. setigera***

1. *Helixanthera alata* (Tiegh.) Danser

Helixanthera alata (Tiegh.) Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 370. — *Coleobotrys alata* Tiegh., Bull. Soc. Bot. France 41 (1894) 542. — Type: *Beccari 11*, Sumatra, Mt Singgalang.
[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 370].

Glabrous except for the young parts shortly and densely tomentose. *Leaves* subopposite, scattered or spirally arranged; lamina lanceolate to elliptic, 5–8 by 1.5–2.5 cm, attenuate or cuneate at the base to a slender petiole 8–16 mm long, attenuate and acute to shortly rounded at the apex, glossy above, dull below; venation pinnate with the midrib distinct and raised on both sides and the secondary and tertiary veins obscure but numerous and more or less parallel at c. 45° to the midrib. *Inflorescences* at the nodes and also terminal on short leafy shoots, a 1- to 8-flowered raceme; axis 5–70 mm long, distinctly angular; pedicels 25–40 mm long, strongly winged, widened upwards and 3–5 mm wide at the apex. *Ovary* narrowly cylindric, 5–7 mm long; calyx limb c. 1 mm long, erect, irregular at the margin. *Corolla* in mature bud 6-merous, 25–30 mm long, uniformly slender and angular, asymmetrically acute (beak-like) at the apex. *Anther* c. 10 mm long, acute, slightly shorter than the free part of the filament. *Style* reaching to the top of the anthers, uniformly slender and 6-angular, lacking a constriction; stigma about as wide as the style.

Distribution — *Malesia*: Sumatra, known only from Mt Singgalang.

Habitat & Ecology — 1600–2400 m altitude; no hosts recorded.

Note — Closely related to and probably derived from the more widespread *Helixanthera cylindrica*, having closely similar leaf, inflorescence and flower architecture, but very distinct in the long flattened pedicels.

2. *Helixanthera coccinea* (Jack) Danser

Helixanthera coccinea (Jack) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 317. — *Loranthus coccineus* Jack, Mal. Misc. 1 (1820) 8. — Type: *Jack*, Singapore (not located).
[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 374].

Plant dark rusty tomentose on all young parts, the leaves and fruits soon glabrescent. *Leaves* scattered or subopposite; lamina narrowly to broadly ovate, 4–12 by 2.5–7 cm, truncate to slightly cordate at the base to a slender petiole 10–22 mm long, attenuate and shortly rounded or obtuse at the apex, thin, dull on both sides; venation pinnate with the midrib visible above and raised below and a few main laterals faintly visible on both sides. *Inflorescences* at the nodes, a 10–30-flowered raceme; axis 15–70 mm long, slender, flexuose; pedicels 0.5–2 mm long; bracts simple, ovate, c. 1 mm long. *Ovary* urceolate, c. 1.5 mm long; calyx limb c. 0.3 mm long, weakly toothed. *Corolla* in mature bud 4-merous, 4–6.5(–8) mm long, strongly keeled in the lower part, weakly clavate and broadly acute at the apex, greenish or reddish brown to bright red. *Anther* c. 1 mm long, obtuse, nearly as long as the free part of the filament. *Style* 3.5–6(–7.5) mm long, reaching to the top of the anthers, distinctly widened upwards, lacking a constriction; quadrangular; stigma capitate, 1.5 times as wide as the style apex.

Distribution — Andaman Islands, Burma to Vietnam; *Malesia*: Sumatra, Peninsular Malaysia, Singapore, Borneo, Palawan.

Habitat & Ecology — Mostly 0–500 m altitude, rarely to 1800 m; the only recorded host is *Dalbergia*.

3. *Helixanthera crassipetala* (King) Danser

Helixanthera crassipetala (King) Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 376. — *Loranthus crassipetalus* King, J. As. Soc. Beng. 56, ii (1887) 91. — Syntypes: *Scortechini* 363, 521, Perak, Mt Idjou.

Helixanthera dura Danser, Rec. Trav. Bot. Néerl. 31 (1934) 243. — Type: *Richards* 1926, Borneo, Mt Dulit. [For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 376].

Glabrous except for a short red-brown tomentum on the young shoots, inflorescences and flowers in some Bornean specimens. *Leaves* scattered or sometimes subverticillate; lamina broadly elliptic to obovate, 5–10 by 2–6.5 cm, cuneate at the base to a petiole 5–15 mm long, obtuse or rounded at the apex, dull or slightly glossy above, dull below; venation pinnate with the midrib distinct below and the many parallel secondary and tertiary veins obscure but forming a finely striate pattern above. *Inflorescences* at the nodes, a 3–16-flowered raceme or spike; axis 20–60 mm long; pedicels 0–4.5 mm long, up to 2 mm thick; bracts simple, ovate, c. 2 mm long. *Ovary* cylindric, 5–7 mm long; calyx limb spreading, c. 1 mm long. *Corolla* in mature bud 5-merous, 17–22(–28) mm long, inflated up to 4 mm wide at the base, gradually narrowed upwards, robust, acute at the apex, yellow to green or pale orange brown. *Anther* 5–6 mm long, acute, almost as long as the free part of the filament. *Style* 16–25 mm long, reaching beyond the top of the anthers, slender, lacking a constriction, angular; stigma not wider than the style.

Distribution — *Malesia*: Peninsular Malaysia, Borneo.

Habitat & Ecology — 600–2100 m altitude; recorded hosts include *Eugenia* and *Lep-tospermum*.

Note — Closely related to *Helixanthera cylindrica*, differing in its shorter inflorescence, pedicels shorter than the ovary, and mostly shorter corolla wider at the base. The two species are sympatric and the specimens most difficult to place may be hybrids.



Fig. 26. *Helixanthera parasitica* Lour. a. Flower-bearing twig; b. flower bud; c. flower with petals and stamens removed. — *H. cylindrica* (Jack) Danser. d. Twig with leaves and flower buds; e. inflorescence. — *H. setigera* (Korth.) Danser. f. Flower bud; g. flower (a–c: *Backer 25567*; d, e: *Danser 6710*; f: *Teijsmann 1079*; g: *Burkill 12450*). Redrawn from Danser (1931). Scale bars represent 1 cm.

4. *Helixanthera cylindrica* (Jack) Danser

Helixanthera cylindrica (Jack) Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 377; Backer & Bakh. f., Fl. Java 2 (1965) 71. — *Loranthus cylindricus* Jack in Roxb., Fl. Ind., ed. 1, 2 (1824) 213. — Type: Jack, Sumatra (probably not extant).

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 377].

Glabrous except for young internodes and sometimes the inflorescence and flowers sparsely brown tomentose and soon glabrescent. *Leaves* scattered, subopposite or subverticillate; lamina elliptic or ovate, 6–15(–20) by (0.8–)1.5–6 cm, attenuate or cuneate at the base to a petiole 8–15 mm long, irregular at the apex but normally somewhat attenuate and acute, dull or slightly glossy above, dull below; venation pinnate with the midrib distinct on both sides, the lateral veins usually distinct above and the many parallel tertiary veins obscure but forming a finely striate pattern above. *Inflorescences* at the nodes and rarely terminal, a few- to 25-flowered raceme; axis 50–250 mm long, angular; pedicels (1–)5–18(–27) mm long; bracts simple, rounded, 1–1.5 mm long. *Ovary* cylindric, 5–8 mm long; calyx limb spreading, 1–1.5 mm long. *Corolla* in mature bud 5-merous, (15–)22–32(–40) mm long, often slightly inflated up to 3 mm wide in the lower 2–4 mm, gradually narrowed upwards, acute at the apex, mostly orange-red to bright red, sometimes yellow or yellow-green. *Anther* 5–8 mm long, acute, about two thirds as long as the free part of the filament. *Style* 15–32(–38) mm long, reaching to the top of the anthers, uniformly slender throughout and lacking a constriction; stigma capitate, slightly wider than the style. — **Fig. 26d, e.**

Distribution — Burma to Vietnam; *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java, Celebes, Bali.

Habitat & Ecology — Somewhat aggressive, in humid and open forests, often on cultivated trees, 0–2000 m altitude; recorded hosts include *Dalbergia*, *Eugenia*, *Garcinia*, *Hevea*, *Leptospermum*, *Mangifera*, *Parkia*, *Planchonella*, *Schima*, *Tristania*.

Note — Closely related to *Helixanthera alata*, *H. crassipetala* and *H. maxwelliana*. Being the most widespread and least specialized species in the group, it is probably the one from which the others have differentiated.

5. *Helixanthera ligustrina* (Wall.) Danser

Helixanthera ligustrina (Wall.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 317. — *Loranthus ligustrinus* Wall. in Roxb., Fl. Ind., ed. 1, 2 (1824) 219. — Type: Wallich, Nepal.

Loranthus tenuis Merr., Philipp. J. Sc., Bot. 4 (1909) 136. — *Helixanthera tenuis* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 318; Philipp. J. Sc. 58 (1935) 106. — Type: Curran FB 6287, lecto (NY), Luzon, Linao For. Res.; *Herb. Ateneo Manila* 217, syn. Luzon, Rizal.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 21].

Glabrous except for all young parts densely brown tomentose, eventually glabrescent except for the ovary. *Leaves* opposite or sometimes scattered; lamina lanceolate to ovate, mostly 3–7 cm long, mostly 1–2 cm wide, attenuate at the base to a petiole 1–6 mm long, acuminate and acute or shortly rounded at the apex, thin, dull on both sides but slightly darker above; venation pinnate with the midrib and the main laterals distinct above and the midrib prominent below. *Inflorescences* at the nodes, a 2- or 3- (rarely

to 5-)flowered raceme; axis 5–20 mm long, flattened upwards; pedicels 0.2–2 mm long, subumbellately crowded near the tip of the axis; bracts triangular, acute, c. 1 mm long. *Ovary* urceolate, 1–1.5 mm long; calyx limb slightly spreading, entire, c. 0.2 mm long. *Corolla* in mature bud 4-merous, 5–8 mm long, slightly keeled in the lower part, narrowed above, weakly clavate and obtuse at the apex, red or purple. *Anther* 2–2.5 mm long, obtuse, 2 to 3 times as long as the free part of the filament. *Style* 5–7 mm long, reaching to the top of the anthers, conical at the base, uniformly slender above, lacking a constriction; stigma capitate, about twice as wide as the style.

Distribution — Himalayas to southern China and Vietnam; *Malesia*: Philippines (Luzon).

Habitat & Ecology — 200–2400 m altitude; in Malesia the only recorded host is *Diospyros*.

Note — The species is recorded both as an aerial branch-parasite and a terrestrial root-parasite; in Malesia it apparently has the former growth habit.

6. *Helixanthera maxwelliana* (Gibbs) Danser

Helixanthera maxwelliana (Gibbs) Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 380. — *Loranthus maxwellianus* Gibbs, J. Linn. Soc., Bot. 42 (1914) 132. — Type: *Gibbs 4006*, Mt Kinabalu. [For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 380].

Glabrous except for young shoots, inflorescences and flowers shortly red-brown tomentose. *Leaves* alternate or subopposite; lamina lanceolate to elliptic, 4–12(–20) by 1–3(–7) cm, cuneate at the base to a petiole 10–15 mm long, acuminate to shortly attenuate and acute at the apex, lustrous above, more or less dull below; venation pinnate with the midrib distinct on both sides and the many parallel secondary and tertiary veins obscure but forming a finely striate pattern above. *Inflorescences* at the nodes, a 13- to 25-flowered spike; axis 45–55 mm long; bracts simple, rounded, c. 1 mm long. *Ovary* cylindric, 3–4 mm long; calyx limb erect, c. 1 mm long. *Corolla* in mature bud 5-merous, 5–7 mm long, sometimes slightly inflated up to 2 mm wide just above the base, narrowed upwards, acute at the apex, mostly red, rarely yellow to brown. *Anther* c. 2 mm long, acute, about half as long as the free part of the filament. *Style* 4–6 mm long, reaching to the top of the anthers, uniformly slender throughout and lacking a constriction; stigma capitate, slightly wider than the style.

Distribution — *Malesia*: endemic to Sabah.

Habitat & Ecology — 100–1800 m altitude; no hosts recorded.

Note — Closely related to *Helixanthera cylindrica*, differing in its much shorter, sessile flowers.

7. *Helixanthera parasitica* Lour.

Helixanthera parasitica Lour., Fl. Coch. 1 (1790) 142; Backer & Bakh. f., Fl. Java 2 (1965) 71. — Type: *Loureiro s.n.*, Cochinchina.
Phoenicanthemum xestophyllum Miq., Fl. Ind. Bat. 1, 1 (1856) 823. — *Helixanthera xestophylla* (Miq.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 319. — Type: *Korthals s.n.*, Borneo, Kalimantan, Luntuntur.

Helixanthera parviflora Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 384. — Type: *Dabong* 778, Borneo, Sarawak.

Helixanthera sumatrana Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 389. — Type: *Saimoendi* 923, Sumatra, Batang Sungai Manau.

Helixanthera annamica Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 18. — Type: *Poilane* 24792, Vietnam, Annam, Tia-Tia.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 381, 391].

Glabrous except for the inflorescence and flowers hairy when young, soon glabrescent except sometimes for the ovary remaining grey-white tomentose. *Leaves* opposite or subopposite; lamina ovate, 5–18 by 1.5–6(–8) cm, cuneate to truncate at the base to a petiole 5–20 mm long, acuminate and acute at the apex, thin, lustrous or dull on either side; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes, a many-flowered raceme; axis (50–)100–300 mm long; pedicels (0.3–)1–2 mm long, often verticillately clustered; bracts ovate or triangular, sometimes



Fig. 27. *Helixanthera parasitica* Lour. Borneo, W Kalimantan (*Elsener* H 248). Photo A. Elsener, 1973.

with a dorsal transverse fold, obtuse or acute, 0.7–1.5 mm long. *Ovary* campanulate, 1.5–3 mm long; calyx limb entire, spreading, 0.3–0.7 mm long. *Corolla* in mature bud 5-merous, (3–)4–9 mm long, strongly keeled in the lower part, narrowed to a slender neck, clavate and obtuse or rounded at the apex, mostly bright red, rarely almost white. *Anther* 1–2.5 mm long, obtuse, about equal to the free part of the filament. *Style* (2–)3–5(–6) mm long, reaching to the base of the anthers, angular in the lower 1–3 mm below a distinct constriction, more slender above; stigma capitate, hardly wider than the style apex. — **Fig. 26a–c, 27.**

Distribution — Himalayas to southern China and Vietnam; *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java, Philippines.

Habitat & Ecology — Humid and open forests, also cultivated lands, 0–2000 m altitude; recorded hosts include *Aglaiia*, *Castanopsis*, *Casuarina*, *Decaspermum*, *Fagraea*, *Ficus*, *Hevea*, *Hopea*, *Lithocarpus*, *Quercus*, and *Saurauia*.

Note — The species is moderately polymorphic with respect to pedicel and corolla length and the form of the bract. The variation is continuous, without a clear geographic pattern, and subsumes the segregate species recognized by Danser (*Helixanthera annamica*, *H. parviflora*, *H. sumatrana*, *H. xestophylla*).

8. *Helixanthera pulchra* (DC.) Danser

Helixanthera pulchra (DC.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 318. — *Loranthus pulcher* DC., Prodr. 4 (1830) 295. — Type: Wallich, Penang I.

Loranthus pulcher DC. var. *sessiliflora* Ridl., Fl. Malay Penins. 3 (1924) 151. — *Helixanthera apodanthes* Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 371. — Type: Robinson s.n., lecto, see note 3, Perak, Mt Kerbau; Ridley 16093, syn, Pahang, Mt Tahan.

Helixanthera pierrei Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 25. — Type: Pierre 673, Cambodia, Mt Knang-Krepeu.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 384; 16 (1938) 25].

Glabrous except for young inflorescences and flowers sparsely tomentose. *Leaves* spirally arranged, sometimes crowded into false whorls; lamina lanceolate to elliptic or ovate, 10–23 by (2.5–)4–11 cm, cuneate to truncate at the base to a distinct petiole 10–25 mm long, acuminate and acute at the apex, lustrous above, dull below; venation pinnate with the midrib visible above and raised below and the main laterals few and faintly visible above. *Inflorescences* at the nodes, a many-flowered raceme or spike sometimes subtended by an involucre of a few narrow bracts up to 5 mm long; axis (100–)150–250 mm long; pedicels 0–2(–3) mm long; bracts strongly reflexed, with a dorsal spur-like sac, 1–2 mm long. *Ovary* campanulate or depressed barrel-shaped, 1.2–2 mm long and wide, usually with irregular wrinkles or furrows persisting to the young fruit. *Corolla* in mature bud 5-merous, (3.5–)5–7(–8.5) mm long, slender in the middle, weakly clavate and rounded at the apex, reddish yellow to bright red. *Anther* 1–1.5 mm long, obtuse, reflexed, slightly shorter than the free part of the filament. *Style* (2.5–)3–4.5(–5.5) mm long, reaching to the base of the anthers, gradually widened upwards, lacking a constriction, angular; stigma as wide as the style.

Distribution — Southern Burma, Thailand; *Malesia*: Sumatra, Peninsular Malaysia.

Habitat & Ecology — 90–1350 m altitude; recorded hosts include *Eugenia*, *Hopea*, *Lithocarpus*, *Mangifera*, *Memecylon*, and *Microtropis*.

Notes — 1. Closely related to *Helixanthera setigera*, differing in the characters set out in the key. Discrimination between small-flowered forms of the two species is sometimes difficult, possibly owing to introgression or significant commonality in their gene pools.

2. The species is moderately polymorphic with respect to pedicel and corolla length and leaf dimensions. The variation lacks a strong geographic pattern, and subsumes the segregate species recognized by Danser (*H. apodanthes*, *H. pierrei*).

3. Of the two syntypes of the name *Loranthus pulcher* var. *sessiliflora* Ridl., on which *H. apodanthes* Danser was based, *Robinson s.n.* (K) is the most complete specimen, and is accordingly selected as lectotype.

9. *Helixanthera sessiliflora* (Merr.) Danser

Helixanthera sessiliflora (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 318. — *Loranthus sessiliflorus* Merr., Philipp. J. Sc. 1, Suppl. (1906) 188. — Type: *Whitford 1171*, lecto, see note, Luzon, Mt Mariveles; *Elmer 6057*, syn, Luzon, Baguio; *Merrill 4041*, syn, Mindoro, Baco River; *McGregor 125*, syn, Mindoro, Baco River.

Glabrous. *Leaves* opposite; lamina elliptic to obovate, 6–12 by 3–7 cm, cuneate to attenuate at the base to a petiole 5–10 mm long, obtuse or rounded at the apex, dull on both sides; venation pinnate with the midrib prominent and the main laterals somewhat curvinerved and faintly visible on both sides. *Inflorescences* at the nodes, a dense many-flowered spike; axis 20–40 mm long; bracts rounded, very concave, appressed to the axis, c. 0.8 mm long. *Ovary* shortly campanulate, c. 1 mm long; calyx limb erect, c. 0.2 mm long. *Corolla* in mature bud 4- or 5-merous, 3.5–5 mm long, slightly inflated and angular in the lower part, narrowed to a neck, clavate and rounded at the apex, red. *Anther* c. 1 mm long, obtuse, slightly longer than the free part of the filament. *Style* 3–4.5 mm long, reaching to the top of the anthers, uniformly slender throughout or widened upwards, lacking a constriction or sometimes constricted immediately below the stigma; stigma obconic, twice as wide as the style.

Distribution — *Malesia*: Philippines.

Habitat & Ecology — 0–1600 m altitude; the only recorded host is *Citrus*.

Note — The originals of the four syntypes (PNH) are not extant; a specimen of *Whitford 1171* has been seen (US) and is designated lectotype of the species name.

10. *Helixanthera setigera* (Korth.) Danser

Helixanthera setigera (Korth.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 318; Backer & Bakh. f., Fl. Java 2 (1965) 72. — *Loranthus setigerus* Korth., Verh. Bat. Genootsch. 17 (1839) 265. — Type: *Korthals s.n.*, Borneo, Mt Sakumbang.

Phoenicanthemum longissimum Miq., Sumatra (1860) 138. — *Helixanthera longissima* (Miq.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 317. — Type: *Teijsmann 1079*, lecto, see note 2, Sumatra, Bondjol; *Diepenhorst 1379*, syn, Sumatra, Pariaman.

Loranthus validus Ridl., Fl. Malay Penins. 5 (1925) 330. — *Helixanthera valida* (Ridl.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 319. — Type: *Burkill SFN 12450*, Perak, Grik.

Helixanthera carinata Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 373. — [*Loranthus pulcher* Ridl., J. Fed. Mal. States Mus. 8 (1917) 81, non DC.] — Type: *Robinson & Kloss 161*, holo, Sumatra, Mt Kerinci.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 380, 387].

Glabrous except for the inflorescence and flowers sparsely tomentose when young and soon glabrescent. *Leaves* opposite, usually displaced and often subverticillate; lamina lanceolate to ovate, (7–)10–25(–30) by (2.5–)4–9(–11) cm, cuneate to truncate at the base to a distinct petiole (8–)12–35 mm long, usually attenuate or shortly acuminate and acute at the apex, slightly lustrous olive green above, dull light brown below; venation pinnate with the midrib and the main laterals faintly to clearly visible on both sides. *Inflorescences* at the nodes, a many-flowered raceme or spike subtended by an involucre of numerous linear bracts up to 15 mm long; axis (150–)200–500(–850) mm long, 3–5 mm thick in the lower part and attenuate towards the tip; pedicels 0.25–2(–4) mm long, often verticillately clustered; bracts deltoid, very concave, often with a sac-like dorsal protuberance, finely acute, 1.5–3 mm long. *Ovary* cylindric, 3–5 mm long; calyx limb erect, entire, 1–1.5 mm long. *Corolla* in mature bud 5- to 7-merous, (7–)8–12 mm long, not inflated at the base, clavate and rounded at the apex, yellow, orange or red. *Anther* 2–2.5 mm long, obtuse, about equal to the free part of the filament. *Style* (3–)5–8 mm long, reaching to the base of the anthers or lower, gradually widened upwards, lacking a constriction; stigma flat, as wide as the style. — **Fig. 26f, g.**

Distribution — Thailand; *Malesia*: Sumatra, Peninsular Malaysia, Borneo, and Java, doubtfully recorded from Bali.

Habitat & Ecology — 0–3000 m altitude; the only recorded host is *Engelhardia*.

Notes — 1. The species is moderately polymorphic with respect to pedicel and corolla length and the form of the bract. The variation lacks a strong geographic pattern, and subsumes the segregate species recognized by Danser (*H. carinata*, *H. longissima*, *H. valida*).

2. Of the two syntypes of the name *Phoenicanthemum longissimum*, *Teijsmann 1079* (U, sh. 38933) is the most complete specimen, and is accordingly selected as lectotype.

3. For comparison with *Helixanthera pulchra*, see there.

11. *Helixanthera spicata* Danser

Helixanthera spicata Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 389. — Type: *Endert 3567*, Borneo, Kalimantan, Kong Kemul.

Glabrous except for the inflorescence and flowers hairy when young, soon glabrescent. *Leaves* opposite; lamina ovate, 5–10 by 1.5–4 cm, cuneate or truncate at the base to a petiole 10–16 mm long, acuminate and acute at the apex, dull but polished on both sides; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes, a many-flowered spike; axis 60–120 mm long; bracts strongly reflexed, with a dorsal spur-like sac, c. 1 mm long. *Ovary* campanulate, c. 1.5 mm long; calyx limb entire, c. 0.2 mm long. *Corolla* in mature bud 5-merous, 4.5–5.5 mm long, strongly keeled in the lower part, narrowed to a slender neck, clavate and obtuse or rounded at the apex, pinkish to deep red. *Anther* c. 0.5 mm long, obtuse, about equal

to the free part of the filament. *Style* 3–4 mm long, reaching to the base of the anthers, angular in the lower 1–1.5 mm below a weak constriction, more slender above; stigma capitate, 1.5–2 times as wide as the style apex.

Distribution — *Malesia*: Borneo.

Habitat & Ecology — 700–1700 m altitude; the only recorded host is *Quercus*.

Note — Closely related to *Helixanthera parasitica*, differing in the stem internodes strongly flattened, dilated upwards and angular; the bracts having a spur-like sac; the completely sessile flowers; and the style only weakly constricted.

LAMPAS

Lampas Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 291, 320. — Type species: *Lampas elmeri* Danser.

Aerial stem-parasitic shrubs. *Leaves* verticillate; venation pinnate. *Inflorescences* axillary, a subumbellate, subcapitate raceme of spirally arranged dichasia (triads) crowded towards the apex of the axis and subtended by an involucre formed from the enlarged central bracts of the outermost triads; bracts single under each flower. *Corolla* 6-merous, regular, gamopetalous to above the middle. *Anthers* basifixed, immobile. *Style* simple, articulate above the base, with a knob-like stigma. — **Fig. 28.**

Distribution — One species confined to Borneo (Sabah).

Habitat & Ecology — Unknown.

Morphology — The inflorescence is an axillary raceme of shortly pedunculate triads apparently crowded into a tight spiral towards the apex of the axis, although they may actually be in several oblique, many-flowered whorls condensed close together. The bracts are decurrent to the bases of the peduncles of the triads, those of the outer (lowermost) triads being longer and wider, with margins free from the peduncles, and together forming a short imbricate involucre subtending the flowers.

Taxonomy — The genus is closely related to *Decaisnina*, differing primarily in the gamopetalous corolla. For further discussion see Barlow, *Blumea* 38 (1993) 108.

Lampas elmeri Danser

Lampas elmeri Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 320. — [*Loranthus elmeri* Merr., Univ. Calif. Publ. Bot. 15 (1929) 53, non Merr. (1914)]. — Type: *Elmer* 20664, Sabah, Tawao.

Glabrous. *Leaves* quaternate; lamina elliptic to ovate, 9–25 cm long, (3–)7–18 cm wide, truncate or cuneate at the base to a thick winged petiole 10–35 mm long, acuminate and obtuse at the apex, dull on both sides, darker and/or lustrous above; venation pinnate but somewhat flabellate with the midrib and the main laterals distinct and the midrib prominent below. *Inflorescences* at the nodes, a raceme of 10–32 spirally arranged triads with the central flower sessile and the lateral flowers obscurely pedicellate; axis deflexed, 30–70 mm long, 3–5 mm thick, widened distally, with the triads crowded in the distal c. 6 mm; peduncles 1.5–2.5 mm long; pedicels c. 0.2 mm long; outer bracts ovate,

c. 7 mm long, acuminate; inner bracts narrower, c. 9 mm long. *Corolla* in mature bud 6-merous, 32–75(–80) mm long, gradually widened upwards, narrowed to a neck, weakly clavate and acute at the apex, red, usually pale yellow or green above; tube in the open flower 18–50 mm long and the lobes reflexed 6–18 mm higher. *Anther* c. 4 mm long, obtuse, almost twice as long as the free part of the filament. — **Fig. 28.**

Distribution — *Malesia*: Borneo (Sabah).

Habitat & Ecology — Altitude 100–700 m; the only recorded host is a species of the *Dilleniaceae*.

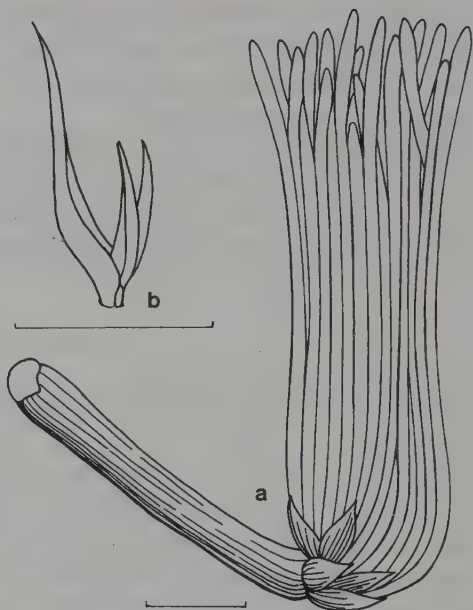


Fig. 28. *Lampas elmeri* Danser. a. Inflorescence, reconstructed from fragments; b. pedicel with bract and bracteoles (Elmer 20644). Redrawn from Danser (1931). Scale bars represent 1 cm.

LEPEOSTEGERES

Lepeostegeres Blume in Schult. & Schult. f., Syst. Veg. 7, 2 (1830) 1611, 1731. — Type species: *Lepeostegeres gemmiflorus* (Blume) Blume.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 258 or Barlow, Austral. J. Bot. 22 (1974) 550].

Aerial stem-parasitic shrubs, often robust, with epicortical runners bearing secondary haustoria. *Leaves* mostly opposite; venation pinnate. *Inflorescences* axillary, an involucrate head composed of 6–12 opposite pairs of dichasia (triads) crowded on the flattened apex of a contracted axis; involucre bracts enlarged, decussate, imbricate, rigid; floral bracts single under each flower. *Corolla* 6-merous, regular, gamopetalous to near the middle. *Anthers* basifixed, immobile, acute. *Style* simple, articulate above the base, usually with a small knob-like stigma. *Fruit* ellipsoid to globular, usually with a persistent nipple-like style base. — **Fig. 29–31.**

Distribution — Endemic to *Malesia*; 9 species distributed from Peninsular Malaysia to New Guinea. The major centre of diversity and species richness is Borneo.

Habitat & Ecology — Humid closed lowland forests to montane and subalpine forests, 0–2800 m altitude; host specificity is probably low.

Morphology — The process of anthesis is unusual and characteristic, the corolla lobes becoming S-shaped at their point of reflexion prior to their separation from each other,

and usually separating downwards before the lobes finally split apart at the apex. In some species it is not certain whether the involuclral bracts are deciduous or persistent after anthesis. For discussion of inflorescence and floral characters see Barlow, *Blumea* 38 (1993) 115.

Taxonomy — Other genera with involuclrate capitate inflorescences, such as *Lepidaria* and *Thaumasianthes*, may not be closely related owing to convergent evolution of this inflorescence state (see Fig. 32, 44). For further discussion on relationships and differences between these genera see Barlow, *Blumea* 38 (1993) 116.

KEY TO THE SPECIES

- 1a. Involuclral bracts acute, sagittate **1. *L. acutibracteus***
- b. Involuclral bracts obtuse to rounded, not sagittate 2
- 2a. Leaves long acuminate and acute at the apex 3
- b. Leaves acute to rounded at the apex but not long acuminate 4
- 3a. Young internodes strongly quadrangular; corolla lobes reflexed at 4/5 the corolla height; free part of the filament less than 10 mm long **9. *L. lancifolius***
- b. Young internodes terete; corolla lobes reflexed at 1/2 to 3/5 the corolla height; free part of the filament more than 10 mm long **3. *L. bahajensis***
- 4a. Involuclral bracts spreading widely after anthesis; flowers in the inflorescence 30 or more **5. *L. centiflorus***
- b. Involuclral bracts remaining appressed after anthesis, or deciduous; flowers in the inflorescence up to 30 5
- 5a. Anther 4–6 mm long, subsessile on free filament up to 1 mm long **2. *L. alveolatus***
- b. Anther 1.5–10 mm long, longer or shorter than a free filament which is more than 1 mm long 6
- 6a. Involuclral bracts deciduous after anthesis 7
- b. Involuclral bracts persistent 8
- 7a. Flowers and fruits sessile; corolla 35–40 mm long **7. *L. deciduus***
- b. Flowers pedicellate, the pedicels elongating under the fruits; corolla 23–32 mm long **6. *L. congestiflorus***
- 8a. Involucre less than 30 mm long; corolla less than 30 mm long; anther 1.5–2 mm long, shorter than the free filament **8. *L. gemmiflorus***
- b. Involucre more than 50 mm long; corolla more than 80 mm long; anther 9–10 mm long, longer than the free filament **4. *L. beccarii***

1. *Lepeostegeres acutibracteus* Danser

Lepeostegeres acutibracteus Danser, *Blumea* 2 (1936) 57. — Type: *Ramos BS 41187*, Philippines, Bu-suanga I.

Glabrous except for the young inflorescence involucre sometimes shortly brown tomentose. *Leaves* opposite; lamina oblong to ovate, 5–18 by 2–7 cm, shortly cuneate or truncate at the base to a winged petiole 3–12 mm long, very slightly acuminate and acute



Fig. 29. *Lepeostegeres*. a. Generalized diagram of inflorescence. — *L. deciduus* Barlow. b. Flower- and fruit-bearing twig. — *L. acutibracteus* Danser. c. Inflorescence with some flowers removed; d. involucral bract from the fourth pair, with pedicels; e. receptacle with innermost involucral bracts, bracteoles, and one flower (b: not cited; c–e: *Ramos BS 41187*). a Redrawn from Danser (1933), b redrawn from Barlow (1981), c–e redrawn from Danser (1936). Scale bars represent 1 cm.

at the apex, glossy above, dull below; venation pinnate with the midrib and the main laterals obscure. *Inflorescences* at the nodes; axis 1–2 mm long, c. 3 mm wide, enlarging in fruit; involucre bracts in c. 5 pairs, the longest inner ones sagittate, keeled, acuminate, 15–23 mm long, spreading and possibly deciduous after anthesis; flowers in 2 or 3 pairs of sessile triads, all with pedicels 1.5–2 mm long. *Corolla* in mature bud 6-merous, 21–45 mm long, slender, gradually widened upwards, obtuse at the apex, red or yellow below, sometimes green above; tube in the open flower 9–18 mm long and the lobes reflexed 7–19 mm higher. *Anther* 1–3 mm long; free part of the filament 0.75–2 mm long. — **Fig. 29c–e.**

Distribution — *Malesia*: Philippines (Palawan).

Habitat & Ecology — 0–660 m altitude; no hosts recorded.

Note — For note on persistence of involucre bracts see Barlow, *Blumea* 38 (1993) 117.

2. *Lepeostegeres alveolatus* (Tiegh.) Danser

Lepeostegeres alveolatus (Tiegh.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 320. — *Stegastrum alveolatum* Tiegh., Bull. Soc. Bot. France 42 (1895) 447. — Type: *Beccari 53*, Celebes, near Kendari. [For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 260].

Glabrous. Stem internodes quadrangular when young. *Leaves* opposite; lamina ovate to obovate, 3–10 by 1.5–8 cm, cuneate at the base to a distinct petiole 8–16 mm long, rounded at the apex, dull on both sides; venation pinnate with the midrib distinct above and raised below and the main laterals obscure above and visible below. *Inflorescences* at the nodes; axis 4–6 mm long, 5–7 mm wide; involucre bracts in 8 or 9 pairs, the longest inner ones narrowly spatulate, 20–30 mm long, spreading somewhat after anthesis; the flowers in 1–3 pairs of sessile triads, all shortly pedicellate. *Corolla* in mature bud 6-merous, 28–33 mm long, slender, gradually widened upwards, obtuse at the apex, red or rarely greenish yellow; tube in the open flower 9–13 mm long and the lobes reflexed 12–14 mm higher. *Anther* 4–6 mm long; free part of the filament 0.5–1 mm long.

Distribution — *Malesia*: Borneo, Celebes.

Habitat & Ecology — 0–1100 m altitude; the only recorded host is a mangrove.

Note — A poorly known species possibly closely related to *Lepeostegeres congestiflorus*; for discussion see Barlow, *Blumea* 38 (1993) 118.

3. *Lepeostegeres bahajensis* (Korth.) Miq.

Lepeostegeres bahajensis (Korth.) Miq., Fl. Ind. Bat. 1, 1 (1856) 833. — *Loranthus bahajensis* Korth., Verh. Bat. Genootsch. 17 (1839) 285. — Type: *Korthals s.n.*, Borneo, Kalimantan. [For guide to additional synonymy see Barlow, *Blumea* 38 (1993) 118].

Glabrous. *Leaves* opposite; lamina narrowly ovate to ovate, (4–)6–10(–15) by (1.5–)2–4.5(–7) cm, truncate at the base to a distinct petiole (6–)10–18 mm long, acuminate and acute at the apex, dull on both sides but darker above; venation pinnate with the midrib distinct above and raised below and the main laterals obscure. *Inflorescences* at the nodes; axis (5–)6–8 mm long, 5–8 mm wide; involucre bracts in 5–8 pairs, the longest

inner ones narrowly spatulate, (20–)25–40(–50) mm long, remaining appressed after anthesis, red; flowers in 3 or 4 pairs of sessile triads, all with pedicels c. 0.5 mm long. *Corolla* in mature bud 6-merous, (30–)40–60 mm long, slender, very slightly inflated at the base, obtuse at the apex, yellow, pink or green, sometimes paler above; tube in the open flower (15–)20–30 mm long and the lobes reflexed 8–20 mm higher. *Anther* 4–7.5 mm long; free part of the filament 10–18(–22) mm long. — **Fig. 31f.**

Distribution — *Malesia*: Borneo.

Habitat & Ecology — Humid forests, mostly at 0–300 m altitude but rarely to 1200 m; recorded hosts include *Gaertnera* and *Syzygium*.

Note — For circumscription as a species see Barlow, *Blumea* 38 (1993) 119.

4. *Lepeostegeres beccarii* (King) Gamble

Lepeostegeres beccarii (King) Gamble, J. As. Soc. Beng. 75, ii (1914) 381. — *Loranthus beccarii* King, J. As. Soc. Beng. 56, ii (1888) 98. — Syntypes: *King's Collector* 7956, Perak; *Beccari PB 1171*, Sarawak.

[For additional synonymy see Danser, *Bull. Jard. Bot. Buitenzorg* III, 11 (1931) 262].



Fig. 30. *Lepeostegeres* prob. *beccarii* (King) Gamble. Borneo, NW Kalimantan, Sanggau. Photo A. Elsener, 1962.

Glabrous. *Leaves* opposite or slightly displaced; lamina narrowly ovate to ovate, 6–16 by 2–6 cm, cuneate to truncate at the base to a petiole 10–25 mm long, mostly obtuse at the apex, dull on both sides; venation pinnate with the midrib distinct above and raised below and the main laterals visible on both sides. *Inflorescences* at the nodes; axis 12–18 mm long, 12–18 mm wide; involucre bracts in 8–11 pairs, the longest inner ones oblong-spathulate, 60–90 mm long, remaining appressed after anthesis, red; flowers in 3 or 4 pairs of sessile triads, all with pedicels c. 0.5 mm long. *Corolla* in mature bud 6-merous, 90–120 mm long, slender, truncate or obtuse at the apex, red, occasionally yellow-green, sometimes yellow above; tube in the open flower 40–60 mm long and the lobes reflexed 35–45 mm higher. *Anther* 9–10 mm long; free part of the filament c. 4 mm long. — **Fig. 30, 31e.**

Distribution — *Malesia*: Sumatra, Peninsular Malaysia, Borneo.

Habitat & Ecology — Humid forests, 0–2150 m altitude; recorded hosts include *Schima*, *Symplocos*, and *Vernonia*.

5. *Lepeostegeres centiflorus* (Stapf) Tiegh.

Lepeostegeres centiflorus (Stapf) Tiegh., Compt. Rend. Acad. Sci. Paris 153 (1911) 1197. — *Loranthus centiflorus* Stapf, Trans. Linn. Soc., Bot. 4 (1894) 222. — Type: *Haviland 1247*, Sabah, Mt Kinabalu. [For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 264].

Glabrous. *Leaves* opposite; lamina narrowly ovate to ovate, (9–)14–18 by (4–)5–8.5 cm, shortly cuneate to slightly cordate at the base to a distinct petiole 9–18 mm long, mostly acute at the apex, lustrous above or dull on both sides; venation pinnate with the midrib distinct above and raised below and the main laterals obscure above and visible below. *Inflorescences* at the nodes; axis 4–10 mm long, c. 8 mm wide; involucre bracts in c. 8 pairs, the longest inner ones spatulate, 25–45 mm long, spreading to 30–70 mm wide after anthesis, green with red midveins; flowers in 5–9 pairs of sessile triads, all with pedicels 1–1.5 mm long. *Corolla* in mature bud 6-merous, 30–75 mm long, slightly inflated above the base, narrowed above, truncate or obtuse at the apex, pink or red or sometimes yellow, sometimes yellow above; tube in the open flower 8–17 mm long and the lobes reflexed 15–40 mm higher. *Anther* 3–6 mm long; free part of the filament 1–3 mm long. — **Fig. 31d.**

Distribution — *Malesia*: Northeastern Borneo.

Habitat & Ecology — Humid forests mostly from 500 to 1700 m altitude, rarely down to 0 m; the only recorded host is *Dryobalanops*.

6. *Lepeostegeres congestiflorus* (Merr.) Merr.

Lepeostegeres congestiflorus (Merr.) Merr., Enum. Philipp. Flow. Pl. 2 (1923) 101. — *Loranthus congestiflorus* Merr., Philipp. J. Sc., Bot. 4 (1909) 147. — Type: *Curran FB 5037*, lecto, Luzon, Mt Tonglon.

Glabrous. *Leaves* opposite or slightly displaced; lamina elliptic to obovate, 5–10 by 2–5 cm, cuneate at the base to an obscure winged petiole 8–15 mm long, rounded at the apex, dull on both sides but darker above; venation pinnate with the midrib distinct above

and raised below and the main laterals obscure. *Inflorescences* at the nodes; axis 3–6 mm long, 3–4 mm wide; involucre bracts in 4–5(–7) pairs, the longest inner ones oblong, 20–25 mm long, deciduous after anthesis; flowers in 3–5 pairs of minutely pedunculate triads, all with pedicels 0.5–2 mm long at anthesis, elongating in fruit. *Corolla* in mature bud 6-merous, 23–32 mm long, slender, very slightly inflated at the base, obtuse at the apex, yellow or green, sometimes red below; tube in the open flower 2.5–5 mm long and the lobes reflexed 12–19 mm higher. *Anther* 3.5–5 mm long; free part of the filament 1–5 mm long.

Distribution — *Malesia*: Philippines.

Habitat & Ecology — (1650–)2000–2800 m altitude; no hosts recorded.

Note — Possibly related to *Lepeostegeres deciduus*; for discussion see Barlow, *Blumea* 38 (1993) 121.

7. *Lepeostegeres deciduus* Barlow

Lepeostegeres deciduus Barlow, Austral. J. Bot. 22 (1974) 550; in Handb. Fl. Papua New Guinea 2 (1981) 245. — Type: *Brass* 31467, Papua New Guinea, Mt Michael.

Glabrous. Stem internodes flattened and double-edged when young. *Leaves* opposite; lamina broadly ovate to obovate, 6–12 by 4–7 cm, cuneate at the base to a winged petiole 5–8 mm long, rounded at the apex, dull on both sides; venation pinnate with the midrib and the main laterals distinct. *Inflorescences* at the nodes; axis 4–5 mm long, 5–7 mm wide; involucre bracts in c. 3 pairs, the longest inner ones oblong, c. 20 mm long, deciduous after anthesis; flowers in 3 or 4 pairs of sessile triads, all sessile. *Corolla* in mature bud 6-merous, 35–40 mm long, slender, acute at the apex, yellowish brown; tube in the open flower 18–24 mm long and the lobes reflexed c. 8 mm higher. *Anther* 4–6 mm long; free part of the filament 3–5 mm long. — **Fig. 29b.**

Distribution — *Malesia*: Papua New Guinea (Eastern Highlands Province).

Habitat & Ecology — Humid forests, (1036–)1500–2000 m altitude; the only recorded host is *Castanopsis*.

Note — For discussion of relationships and biogeography see Barlow, *Blumea* 38 (1993) 122.

8. *Lepeostegeres gemmiflorus* (Blume) Blume

Lepeostegeres gemmiflorus (Blume) Blume in Schult. & Schult. f., Syst. Veg. 7, 2 (1830) 1611; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 266; Backer & Bakh. f., Fl. Java 2 (1965) 69; Barlow, *Blumea* 38 (1993) 122. — *Loranthus gemmiflorus* Blume, Verh. Bat. Genootsch. 9 (1823) 187. — *Elytranthe gemmiflora* (Blume) G. Don, Gen. Hist. 3 (1834) 427. — Type: *Blume s. n.*, Java, Cibodas.

Glabrous. Stem internodes quadrangular when young. *Leaves* opposite; lamina ovate, 5–8 by 2–5 cm, truncate at the base to a distinct petiole 10–20 mm long, rounded or obtuse at the apex, dull on both sides; venation pinnate with the midrib distinct above and raised below and the main laterals visible on both sides. *Inflorescences* at the nodes; axis c. 5 mm long, 5–7 mm wide; involucre bracts in 7–9 pairs, the longest inner ones oblong, 14–20 mm long, remaining appressed after anthesis; flowers in 2–4 pairs of

sessile triads, all with pedicels 0.2–0.3 mm long. *Corolla* in mature bud 6-merous, 20–26 mm long, gradually widened upwards, obtuse at the apex, red or orange or yellow, sometimes greenish yellow above and/or crimson at the tip; tube in the open flower c. 8 mm long and the lobes reflexed 7–12 mm higher. *Anther* 1.5–2 mm long; free part of the filament 2–5 mm long.

Distribution — *Malesia*: Java (Western part).

Habitat & Ecology — 200–1600 m altitude; recorded hosts include *Erythrina*, *Ficus*, and *Ixora*.

9. *Lepeostegeres lancifolius* (Tiegh.) Danser

Lepeostegeres lancifolius (Tiegh.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 321. — *Stegastrum lancifolium* Tiegh., Bull. Soc. Bot. France 42 (1895) 447. — Type: *Beccari* 537, Sarawak, Kuching. [For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 269].

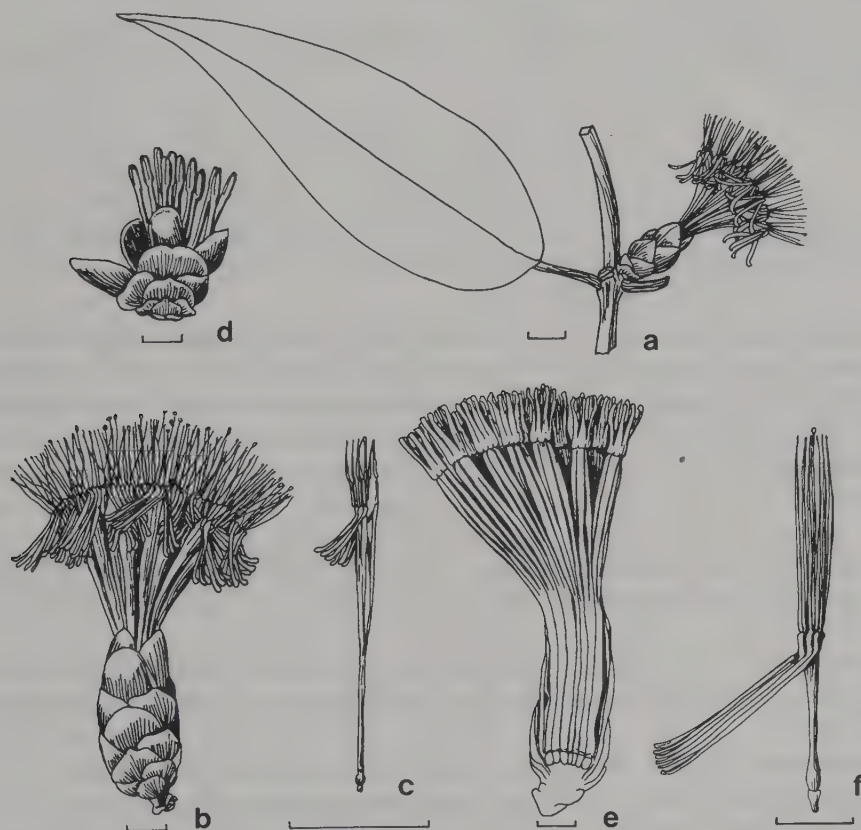


Fig. 31. *Lepeostegeres lancifolius* (Tiegh.) Danser. a. Flower-bearing portion of stem; b. inflorescence; c. flower. — *L. centiflorus* (Stapf) Tiegh. d. Inflorescence with most flower buds removed. — *L. beccarii* (King) Gamble. e. Inflorescence in sectional view. — *L. bahajensis* (Korth.) Miq. f. Flower (a: Haviland 1676; b, c: Amdjah 1095; d: Elmer 21083; e: Endert 2367; f: Haviland 536). Redrawn from Danser (1931). Scale bars represent 1 cm.

Glabrous. Stem internodes quadrangular when young. *Leaves* opposite; lamina narrowly ovate to ovate, 9–25 by 3–12 cm, shortly cuneate to slightly cordate at the base to a distinct petiole 12–28 mm long, acuminate and acute at the apex, glossy above, dull below; venation pinnate with the midrib distinct above and raised below and the main laterals obscure. *Inflorescences* at the nodes; axis 4–10 mm long, 6–7 mm wide; involucre bracts in (6–)8–12 pairs, the longest inner ones spatulate, (22–)25–45(–55) mm long, remaining appressed after anthesis, red; flowers in 2–4 pairs of sessile triads, all with pedicels 0.5–1.5 mm long. *Corolla* in mature bud 6-merous, (42–)50–75(–100) mm long, very slender, obtuse at the apex, red or rarely orange or green, sometimes with yellow-green above and then sometimes red at the tip; tube in the open flower 10–30 mm long and the lobes reflexed 10–30 mm higher. *Anther* 3–10 mm long; free part of the filament 6–10 mm long. — **Fig. 31 a–c.**

Distribution — *Malesia*: Borneo.

Habitat & Ecology — Humid forests from 0 to 400 m altitude; the only recorded host is *Koompassia*.

Note — Similar to *Lepeostegeres beccarii*; for differences see Barlow, *Blumea* 38 (1993) 123.

LEPIDARIA

Lepidaria Tiegh., Bull. Soc. Bot. France 42 (1895) 439. — Type species: *Lepidaria bicarinata* Tiegh. [For synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 308; *Blumea* 2 (1936) 35; and note under Morphology & Taxonomy below].

Aerial stem-parasitic shrubs, often robust, with epicortical runners bearing secondary haustoria. *Leaves* opposite. *Inflorescences* axillary, a more or less sessile involucre head of 1–few decussate pairs of flowers on a short floral axis; involucre bracts decussate, enlarged, rigid, often keeled, brightly coloured, imbricate, tightly enclosing the developing flowers, the lower ones sterile and the upper ones subtending the flowers; lateral bracts 2 enclosing each flower. *Corolla* mostly 6-merous, gamopetalous, regular or nearly so, often more deeply split on one side. *Anthers* basifixed, immobile, often spurred at the base. *Style* simple, conical at the base, articulate above the base, with a knob-like stigma. *Fruit* ellipsoid to obovate. — **Fig. 32.**

Distribution — Genus of 8 species, endemic to northern and western *Malesia* except for 1 species which reaches peninsular Thailand. The centre of species richness is Borneo.

Habitat & Ecology — Mostly closed humid forests, ranging from lowlands to high montane communities at up to 3550 m altitude; host specificity is generally low.

Morphology & Taxonomy — Danser realigned *Macrosolen*, *Elytranthe* and *Lepidaria* in *Blumea* 2 (1936) 35, transferring *E. arnottiana* to *Lepidaria*, and reinstating the genus *Lepidella* for several species of *Lepidaria* (see notes under *Macrosolen* and *Elytranthe*). However, the basic generic character is the involucre of sterile, imbricate floral bracts

subtending an essentially capitate sessile inflorescence, and *Lepidaria* and *Lepidella* share this character and belong together. *Lepidella* represents the extreme in inflorescence reduction and compaction, with the 2 remaining pairs of flowers on a relatively flat receptacle, whereas in *Lepidaria* there are more pairs of flowers and the receptacle is stepped accordingly. *Lepidaria* (sens. lat.) is clearly distinct from *Elytranthe* (including *E. arnottiana*), where the inflorescence is a well-developed spike in which the function of the involucre is provided by the floral bracts.

KEY TO THE SPECIES

- 1a. Inflorescence of 6 or more pairs of flowers 2
- b. Inflorescence of 1–4 pairs of flowers 3
- 2a. Involucre c. 70 mm long; leaf lamina dark coloured at the margin, 9–15 cm long **3. *L. oviceps***
- b. Involucre 35–50 mm long; leaf lamina not dark coloured at the margin, 12–24 cm long **1. *L. bicarinata***
- 3a. Corolla more than 60 mm long; involucre more than 50 mm long **2. *L. kingii***
- b. Corolla 32–60 mm long; involucre 18–30 mm long 4
- c. Corolla less than 30 mm long; involucre less than 18 mm long 6
- 4a. Leaf lamina more than 9 cm long; involucre bracts strongly recurved at the apex .. **4. *L. pulchella***
- b. Leaf lamina less than 9 cm long; involucre bracts not or only slightly recurved at the apex 5
- 5a. Stem internodes angular or ridged longitudinally; leaf lamina broadly acute at the apex **6. *L. sabaensis***
- b. Stem internodes terete; leaf lamina obtuse or rounded **8. *L. vaginata***
- 6a. Involucre bracts thin, flexible, acuminate and acute **7. *L. tetrantha***
- b. Involucre bracts rigid, rounded at the apex **5. *L. quadriflora***

1. *Lepidaria bicarinata* Tiegh.

Lepidaria bicarinata Tiegh., Bull. Soc. Bot. France 42 (1895) 440 ('*bicarenata*'). — Type: *Beccari 910*, Sarawak, Kuching.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 309].

Glabrous. *Leaves* opposite; lamina ovate to rarely obovate, 12–24 by 5–11 cm, cuneate at the base to a petiole 8–20 mm long, attenuate and finally acute to rounded at the apex, lustrous or dull green above, dull and brownish below; venation pinnate with the midrib and the main laterals distinct on both sides and the midrib prominent and often dark coloured below. *Inflorescences* at the nodes, a subsessile involucre capitate spike of usually 6 decussate pairs of flowers; involucre 35–50 mm long, mostly red, sometimes yellow at the base, comprising c. 14 pairs of bracts, the longer ones keeled, smooth or slightly undulate below the apex; floral axis 5–10 mm long; lateral bracts enclosing

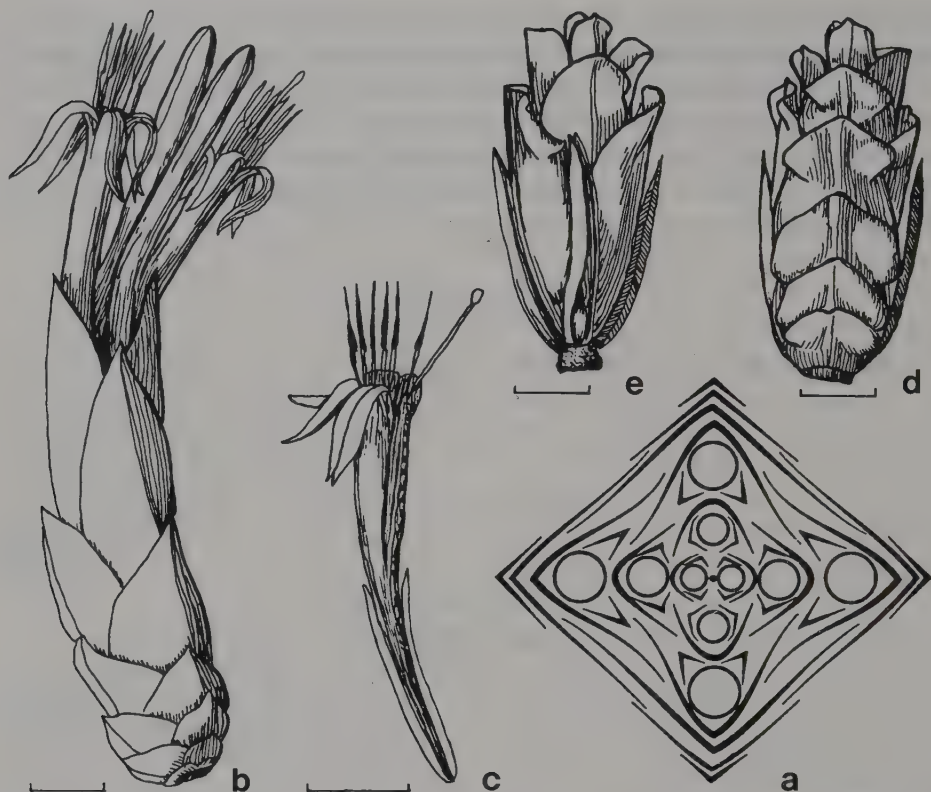


Fig. 32. *Lepidaria*. a. Generalized diagram of inflorescence. — *L. kingii* (King) Danser. b. Inflorescence; c. flower with bracteoles. — *L. bicarinata* Tiegh. d. Inflorescence; e. inflorescence, partly dissected (b: Burkill & Holttum 8692; c: Ridley 10771, d, e: not cited). a Redrawn from Danser (1933), b–e redrawn from Danser (1931). Scale bars represent 1 cm.

the flowers c. 25 mm long, keeled, acute. *Corolla* in mature bud 6-merous, 60–70 mm long, gradually widened upwards, winged above the middle to the acute or obtuse apex, mostly red or yellow below, yellow-green above; tube in the open flower 45–50 mm long, split slightly deeper on one side, with the lobes reflexed and twisted c. 5 mm higher. *Anther* c. 5 mm long, spurred at the base, acute, about half as long as the free part of the filament. — **Fig. 32d, e.**

Distribution — *Malesia*: Sumatra, Borneo (Sarawak).

Habitat & Ecology — Foothills to 860 m altitude; the only recorded host is *Xanthophyllum*.

Note — Van Tieghem's derivation of the original spelling of the specific epithet from the French 'carène' (keel) was apparently an unintentional error, and was validly corrected by later authors.

2. *Lepidaria kingii* (King) Danser

Lepidaria kingii (Scort. ex King) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 322. — *Loranthus kingii* Scort. ex King, J. As. Soc. Beng. 56, ii (1887) 99. — *Lepidella kingii* (Scort. ex King) Danser, Blumea 2 (1936) 37. — Type: *Scortechini 1251*, Perak.

Loranthus forbesii King, J. As. Soc. Beng. 56, ii (1887) 100. — *Lepidaria forbesii* (King) Tiegh., Bull. Soc. Bot. France 42 (1895) 441. — *Lepidella forbesii* (King) Danser, Blumea 2 (1936) 37. — Type: *Forbes 2844*, Sumatra, Kepala Curup.

Lepidaria malaiana Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 314. — *Lepidella malaiana* (Danser) Danser, Blumea 2 (1936) 37. — Type: *Burkill & Holttum 8692*, Malaya, Fraser Hill.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 310, 312].

Glabrous. *Leaves* opposite; lamina narrowly ovate to ovate, 9–20 by 3.5–11 cm, shortly cuneate to slightly cordate at the base to a petiole 10–30 mm long, attenuate or acuminate and usually acute at the apex, dull on both sides or slightly lustrous above; venation pinnate with the midrib and the main laterals visible on both sides and the midrib prominent below. *Inflorescences* at the nodes, a sessile involucre capitate spike of usually 2 decussate pairs of flowers; involucre 50–85 mm long, red, comprising 6–10 pairs of bracts, the upper ones oblong, keeled, acute, very slightly and finely undulate near the apex; floral axis 4–8 mm long; lateral bracts enclosing the flowers 15–30 mm long, keeled, acute. *Corolla* in mature bud 6-merous, 60–115(–130) mm long, widened upwards for three fourths its length, weakly winged below the neck, clavate acute to obtuse at the apex, yellow to red, ribbed with yellow to red; tube in the open flower 45–90 mm long, with 1 or 2 deeper splits on one side, with the lobes reflexed 3–6 mm higher. *Anther* 5–8 mm long, slightly spurred at the base, acute, slightly shorter to slightly longer than the free part of the filament. — **Fig. 32b, c.**

Distribution — Peninsular Thailand; *Malesia*: Sumatra, Peninsular Malaysia, Borneo.

Habitat & Ecology — 0–1680 m altitude; the only recorded host is *Vitex*.

Note — The difference in corolla symmetry used by Danser to distinguish *Lepidaria forbesii* and *L. malaiana* from *L. kingii* is only a transitory feature of anthesis. Corolla length is often longer in Bornean specimens than in Peninsular Malaysian ones, but the differences cited by Danser to distinguish these taxa do not exist. Even when *L. kingii* is circumscribed to include *L. forbesii* and *L. malaiana*, the species is not very polymorphic.

3. *Lepidaria oviceps* Danser

Lepidaria oviceps Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 315. — Type: *Hallier B 1945*, Kalimantan, Mt Kenepai.

Glabrous. *Leaves* opposite, sometimes displaced; lamina broadly ovate, 9–15 by 7–10 cm, shortly cuneate to truncate at the base to a petiole 8–20 mm long, thick, dark coloured at the margin, rounded at the apex, dull on both sides; venation pinnate with the midrib dark coloured and raised on both sides and the main laterals obscure. *Inflorescences* at the nodes, a sessile involucre capitate spike of 6 or more decussate pairs of flowers; involucre c. 70 mm long, red, comprising c. 15 pairs of bracts, the upper ones oblong, obtuse, smooth, weakly keeled only near the apex; floral axis c. 6 mm

long; lateral bracts enclosing the flowers c. 30 mm long, keeled, obtuse. *Corolla* in mature bud and open flower not known.

Distribution — *Malesia*: Borneo.

Habitat & Ecology — Low altitudes; the only recorded host is *Gonostylus*.

4. *Lepidaria pulchella* Danser

Lepidaria pulchella Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 315. — Type: *Clemens* 21837, Sarawak, Upper Rejang River.

Glabrous or young parts scurfy. *Leaves* opposite, sometimes displaced; lamina ovate to elliptic, 10–20 by 5–10 cm, cuneate at the base to a petiole 10–20 mm long, attenuate and finally acute to rounded at the apex, lustrous or dull green above, dull and brownish below; venation pinnate with the midrib and the main laterals distinct on both sides and the midrib prominent below. *Inflorescences* at the nodes, a subsessile involucrate capitate spike of 2–3(–4) decussate pairs of flowers; involucre 20–30 mm long, mostly yellow or green below and orange or red above, comprising 10–12 pairs of bracts, the longer ones keeled, mostly strongly recurved along the upper margin; floral axis c. 5 mm long; lateral bracts enclosing the flowers c. 12 mm long, keeled, acute. *Corolla* in mature bud 6-merous, 45–60 mm long, gradually widened upwards, winged above the middle to the acute or obtuse apex, mostly red, usually streaked with white or yellow; tube in the open flower 32–45 mm long, with the lobes reflexed and twisted 3–5 mm higher. *Anther* 4–5 mm long, spurred at the base, acute, about three fourths as long as the free part of the filament.

Distribution — *Malesia*: Borneo (Sarawak, Brunei, Sabah).

Habitat & Ecology — Common from 0 to 1500 m altitude; recorded hosts include *Drypetes*, *Shorea*, and *Vatica*.

Note — Vegetatively similar to *Lepidaria bicarinata*, but differs in its fewer-flowered inflorescences with smaller involucres in which the bracts are more undulate or rolled back at the margins.

5. *Lepidaria quadriflora* Tiegh.

Lepidaria quadriflora Tiegh., Bull. Soc. Bot. France 42 (1895) 441. — *Lepidella quadriflora* (Tiegh.) Danser, Blumea 2 (1936) 37. — Type: *Cuming* 1971, Philippines, 'Manille'.

Loranthus williamsii Merr., Philipp. J. Sc., Bot. 4 (1909) 148. — *Lepidaria williamsii* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 322. — *Lepidella williamsii* (Merr.) Danser, Blumea 2 (1936) 37. — Type: *Williams* 973, Luzon, Baguio.

[For additional synonymy see Danser, Blumea 3 (1940) 394].

Glabrous. *Leaves* opposite; lamina narrowly ovate to elliptic, sometimes falcate, 5–8 by 1–3 cm, cuneate to attenuate at the base to an obscure petiole 1–7 mm long, attenuate and rounded at the apex, dull on both sides; venation pinnate with the midrib and the main laterals visible on both sides and the midrib prominent below. *Inflorescences* at the nodes, an involucrate capitate spike of usually 2 decussate pairs of flowers on a pedun-

cle 1–2 mm long; involucre 13–18 mm long, comprising 5 or 6 pairs of bracts, the upper ones broadly elliptic, smooth, rounded, deciduous at anthesis; floral axis 0.5–1 mm long; lateral bracts enclosing the flowers vestigial. *Corolla* in mature bud 5- or 6-merous, 22–33 mm long, gradually widened upwards, slightly narrowed above the middle to a neck, weakly clavate, angular and obtuse at the apex, red; tube in the open flower variable, 3.5–20 mm long, more deeply split on one side, with the lobes reflexed 3–20 mm higher. *Anther* 3.5–5.5 mm long, acute, 1–4 times as long as the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — No habitat details or hosts recorded.

6. *Lepidaria sabaensis* (Stapf) Danser

Lepidaria sabaensis (Stapf) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 322. — *Loranthus sabaensis* Stapf, Trans. Linn. Soc., Bot. 4 (1894) 222. — *Lepidella sabaensis* (Stapf) Tiegh., Compt. Rend. Acad. Sci. 153 (1911) 1198. — Type: *Haviland 1079*, lecto, see note, Borneo, Mt Kinabalu.

Glabrous. Stem internodes compressed upwards, angular or longitudinally ridged. *Leaves* opposite; lamina ovate, 3.5–6 by 1.7–3 cm, cuneate to truncate at the base to a petiole 5–10 mm long, broadly acute at the apex, dull on both sides or slightly lustrous above; venation pinnate with the midrib raised below and other veins obscure. *Inflorescences* at the nodes, a sessile involucre capitate spike of usually 2 decussate pairs of flowers; involucre 18–22 mm long, pink to red, comprising c. 7 pairs of bracts, the upper ones broadly elliptic, keeled, otherwise smooth or slightly recurved near the apex, spreading at anthesis; floral axis c. 3 mm long; lateral bracts enclosing the flowers c. 15 mm long, keeled, obtuse. *Corolla* in mature bud 6-merous, 32–45 mm long, widened upwards, winged near the middle, clavate above a neck and angular and obtuse at the apex, orange or red below, green at the neck and yellow above; tube in the open flower 16–32 mm long, more deeply split on one side, with the lobes reflexed or twisted slightly higher. *Anther* c. 4 mm long, spurred at the base, acute, about half long as the free part of the filament.

Distribution — *Malesia*: Borneo (Sabah: Mt Kinabalu).

Habitat & Ecology — Mostly 3000–3550 m altitude, less often down to 2440 m; recorded hosts include *Leptospermum*, *Rhododendron*, and *Vaccinium*.

Note — In the original description of *Loranthus sabaensis* Stapf cited two collections, *Haviland 1079* & *1108*, which are therefore syntypes. Of the two specimens in K, the former bears more flowering material and is accordingly chosen as lectotype of the species name.

7. *Lepidaria tetrantha* (Merr.) Danser

Lepidaria tetrantha (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 322. — *Loranthus tetranthus* Merr., Philipp. J. Sc., Bot. 7 (1912) 79. — *Lepidella tetrantha* (Merr.) Danser, Blumea 2 (1936) 37. — Type: *Vanoverbergh 1294*, lecto, see note, Luzon, Malawey.

[For additional synonymy see Danser, Blumea 3 (1940) 394].

Glabrous. Stem internodes slightly compressed-angular. *Leaves* opposite; lamina ovate to elliptic, 5–7 by 1.5–2.5 cm, cuneate at the base to a petiole 3–5 mm long, attenuate or acuminate and acute to shortly rounded at the apex, dull green above, dull brown below; venation pinnate with the midrib distinct below and other veins obscure. *Inflorescences* at the nodes, a sessile involucre capitate spike of usually 2 decussate pairs of flowers; involucre 10–13 mm long, comprising c. 10 pairs of bracts, the upper ones narrowly ovate, thin, acuminate and acute, deciduous at anthesis; floral axis c. 0.5 mm long; lateral bracts vestigial. *Corolla* in the mature bud 6-merous, c. 22 mm long, widened upwards in the lower part, angular below the middle, weakly clavate above a long neck and acute at the apex, red below and green above; tube in the open flower 3–4 mm long with the lobes reflexed close to the apex. *Anther* c. 3 mm long, acute, about twice as long as the free part of the filament.

Distribution — *Malesia*: Philippines (Luzon).

Habitat & Ecology — Highlands; no host recorded.

Note — The holotype of *Loranthus tetranthus* (PNH) is no longer extant. An isotype (US, 900071) has been seen and designated lectotype of the species name.

8. *Lepidaria vaginata* Tiegh.

Lepidaria vaginata Tiegh., Bull. Soc. Bot. France 42 (1895) 440. — *Lepidella vaginata* (Tiegh.) Tiegh., Compt. Rend. Acad. Sci. 153 (1911) 1198. — Type: *Beccari* 2579, Borneo, Mt Matang. [For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 318].

Glabrous. *Leaves* opposite; lamina elliptic or ovate, 5–8 by 3–6 cm, cuneate to truncate at the base to a petiole 10–20 mm long, obtuse or rounded at the apex, slightly lustrous above or dull on both sides; venation pinnate with the midrib distinct above and raised and dark coloured below and the main laterals distinct on both sides or obscure below. *Inflorescences* at the nodes, a sessile involucre capitate spike of 1 or 2 decussate pairs of flowers; involucre 20–25 mm long, comprising 8–10 pairs of bracts, the upper ones elliptic, obtuse, smooth except for the weakly keeled upper part, green below and brown above; floral axis c. 2.5 mm long; lateral bracts enclosing the flowers c. 12 mm long, keeled, broadly acute. *Corolla* in mature bud 6-merous, c. 50 mm long, slender in the lower 6–7 mm, with deflexed spurs inside forming a nectar chamber, widened above, winged just above the middle, clavate above a neck and acute at the apex, red, usually streaked with yellow; tube in the open flower 35–40 mm long, more deeply split on one side, with the lobes reflexed slightly higher. *Anther* 3–3.5 mm long, acute, about two thirds as long as the free part of the filament.

Distribution — *Malesia*: Borneo, known only from Mt Matang.

Habitat & Ecology — 500–800 m altitude; no hosts recorded.

LORANTHUS

Loranthus L., Sp. Pl. (1753) 351, *nom. cons.* — *Hyphear* Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 292, 319. — Type species: *Loranthus europaeus* Jacq. (see note). [For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 26, under *Hyphear*].

Aerial stem-parasitic shrubs, sometimes with epicortical runners bearing secondary haustoria. *Leaves* opposite or displaced. *Inflorescence* a simple spike; bracts single under each flower. *Flowers* probably mostly functionally unisexual but usually with organs of the other gender present, either apparently normally developed or vestigial. *Corolla* 4- to 6-merous, small, choripetalous, regular or nearly so. *Anthers* basifixed, immobile. *Style* straight, simple. *Fruit* nearly globular. — **Fig. 33.**

Distribution — Probably 2 species, from southeastern Europe to southern Asia as far as Japan. In *Malesia* 1 species, known from Sumatra and Celebes.

Habitat & Ecology — Mostly temperate or montane deciduous or evergreen forests; host specificity is probably high for *Quercus*, although *Pinus* and other hosts are also parasitized.

Taxonomy — In this genus several species have been distinguished on the basis of number of petals, and on plants being apparently dioecious or hermaphrodite. These variations have little systematic value; see Danser, *Blumea* 2 (1936) 44. The two species now accepted have robust differences in inflorescence insertion and structure.

Loranthus is very closely related to the larger genus *Helixanthera*, which extends from Africa to southern Asia and northwestern Malesia. *Helixanthera* is relatively polymorphic, with a few species groups which differ strikingly from each other in flower size, relative style length and presence or absence of an articulation in the style. It is difficult to discriminate *Loranthus* as an entity with differences greater than those which distinguish the groups within *Helixanthera*. The presence of unisexual flowers has sometimes been used to distinguish *Loranthus*, but the character appears to be variable even within the species of the genus. Danser [Bull. Jard. Bot. Buitenzorg III, 16 (1938) 26] accordingly expressed the view that *Loranthus* (*Hyphear*) and *Helixanthera* are congeneric. Further study is needed to resolve this issue, as the taxonomic consequence of uniting the genera would be the submergence of the larger genus *Helixanthera* into the very small genus *Loranthus*. For further discussion, see Barlow, *Blumea* 40 (1995) 24–25. Ban, Tap Chi Sinh HOC 16, 4 (1994) 48, 54, has without discussion apparently proposed union of these two genera. However, he has overlooked the nomenclatural conservation of *Loranthus*, and has accordingly placed *Hyphear* (1929) in synonymy under *Helixanthera* (1790).

Note — The originally designated type species of *Loranthus*, *L. americanus*, is referable to the large American genus *Psittacanthus*. The usual application of the name *Loranthus* has been restored by conservation, with the well-known *L. europaeus* nominated as type; the usual application of the name *Psittacanthus* is accordingly also retained.

***Loranthus odoratus* Wall.**

Loranthus odoratus Wall. in Roxb., Fl. Ind., ed. 1, 2 (1824) 215. — *Hyphear odoratum* (Wall.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 319. — Type: *Wallich s.n.*, India, 'Mountains of Chanda-giri and Sheopore'.

Loranthus delavayi Tiegh., Bull. Soc. Bot. France 41 (1984) 535. — *Hyphear delavayi* (Tiegh.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 319. — *Helixanthera delavayi* (Tiegh.) Ban, Tap Chi Sinh HOC 16, 4 (1994) 48. — Syntypes: *Delavay* 2312, 3667, 4653, Yunnan, Mounghan.

Glabrous. Stem internodes dilated upwards. *Leaves* opposite or subopposite; lamina narrowly ovate to ovate, 5–10 by 1.5–3 cm, attenuate or cuneate at the base to a sometimes obscurely defined petiole up to 20 mm long, acuminate and acute at the apex, dull on both sides or slightly lustrous above; venation pinnate with the midrib and the main laterals distinct on both sides and more prominent below. *Inflorescences* at the nodes, a many-flowered spike; axis 15–80 mm long, with the flowers inserted in shallow hollows. *Flowers* probably functionally unisexual but often with vestigial organs of the other sex. *Corolla* in mature bud 6-merous, 3–4 mm long, widened upwards, clavate and rounded at the apex, white, yellow or orange. *Anther* c. 1 mm long, obtuse, about equal to the free part of the filament. — **Fig. 33.**

Distribution — Nepal to southern China and Taiwan; *Malesia*: Sumatra, Celebes, and known from only two collections.

Habitat & Ecology — Mostly 1000–3000 m altitude; frequently parasitic on *Quercus*; in Malesia recorded once from oak-myrtle forest, parasitic on *Lithocarpus*.

Note — For discussion on further likely synonymy, see Danser, *Blumea* 2 (1936) 44; Bull. Jard. Bot. Buitenzorg III, 16 (1938) 27.

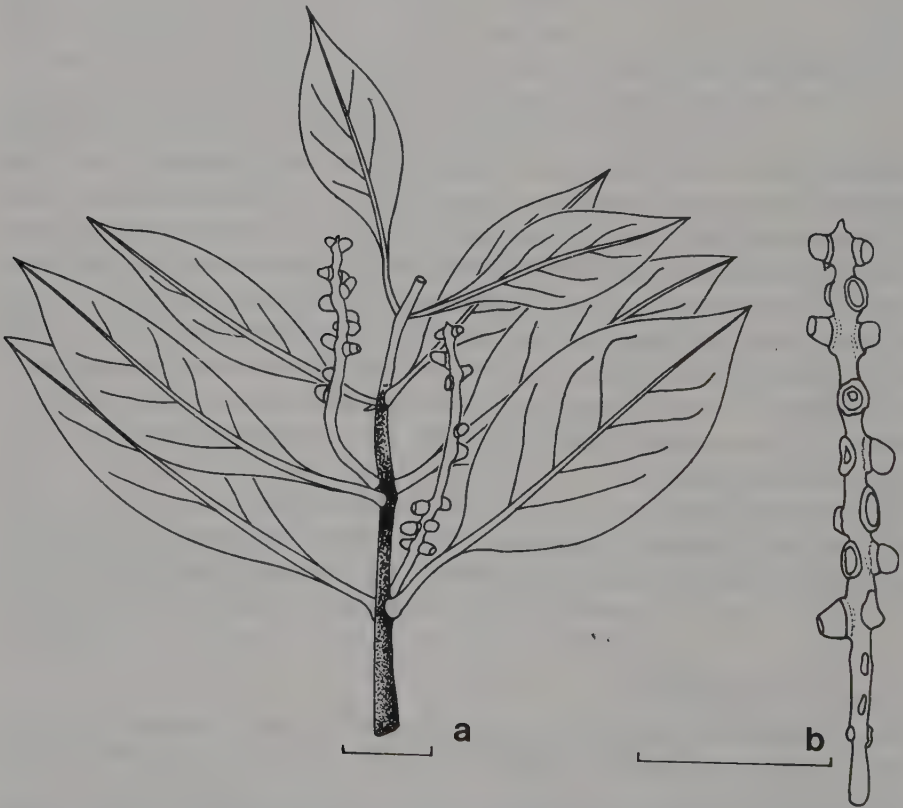


Fig. 33. *Loranthus odoratus* Wall. a. Twig with fruiting inflorescences; b. fruiting inflorescence (*Nicolson* 3041). Drawing Sandie McIntosh. Scale bars represent 1 cm.

LOXANTHERA

Loxanthera Blume in Schult. & Schult. f., Syst. Veg. 7, 2 (1830) 1612, 1730. — Type species: *Loxanthera speciosa* Blume

Aerial stem-parasitic shrubs with epicortical runners bearing secondary haustoria. *Leaves* opposite; venation pinnate. *Inflorescences* axillary, a raceme of decussate pairs of pedunculate dichasia (triads); bracts single under each flower. *Corolla* 6-merous, regular, gamopetalous to above the middle. *Anther* immobile, introrse, with an extension from the base which is free from the filament so that the filament appears dorsifixed. *Style* simple, articulate at the base, with a knob-like stigma. *Fruit* ellipsoid. — **Fig. 34.**

Distribution — Endemic to *Malesia*; 1 species distributed in western Malesia.

Habitat — Humid forests, possibly with high host specificity for *Ficus*.

Morphology — The distinctive feature of *Loxanthera* is the apparently dorsifixed, immobile introrse anther (see Fig.34). For discussion, see Barlow, Blumea 38 (1993) 114.

Taxonomy — The genus is possibly related to *Amylothea*, differing primarily in the specialized anther structure. It is a member of the *Decaishnina* group of genera, differing from the latter also by its gamopetalous corolla. For further discussion see Barlow, Blumea 38 (1993) 114.

Loxanthera speciosa Blume

Loxanthera speciosa Blume in Schult. & Schult. f., Syst. Veg. 7, 2 (Oct.-Dec. 1830) 1612, 1649, 1730; Backer & Bakh. f., Fl. Java 2 (1965) 69; Barlow, Blumea 38 (1993) 115. — *Loranthus loxantherus* DC., Prodr. 4 (Sep. 1830) 316. — [*Loxanthera loxanthera* (DC.) Danser, Verh. Akad. Wet. Amst. Afd. Natuurk. 29, sect. 2 (1933) 90, nom. inval.] — Type: *Blume s.n.* (probably collected by Reinwardt), Java.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 254].

Glabrous. *Leaves* opposite; lamina narrow ovate to ovate, 6–14 by 2.5–8 cm, thick, shortly cuneate to slightly cordate at the base to a petiole 5–20 mm long, weakly acuminate and mostly acute at the apex, usually glossy above, dull below; venation pinnate with the midrib distinct and the main laterals obscure on both sides and the midrib prominent below. *Inflorescences* at the nodes, a raceme of 1–3 decussate pairs of triads with all flowers pedicellate; axis 5–15 mm long; peduncles of the triads 5–10 mm long; pedicels of the flowers 5–7 mm long. *Corolla* in mature bud 6-merous, 80–140 mm long, robust, inflated at the base, gradually widened upwards, clavate and usually obtuse at the apex, pink or red in the lower part, sometimes black at the apex; tube in the open flower 50–95 mm long. *Anther* 5–8 mm long, curved, attached at about one third its length, acute at the base, obtuse at the apex, much shorter than the free part of the filament. — **Fig. 34.**

Distribution — *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java.

Habitat & Ecology — Humid forests, 0–1600 m altitude; only recorded as parasitic on *Ficus*.

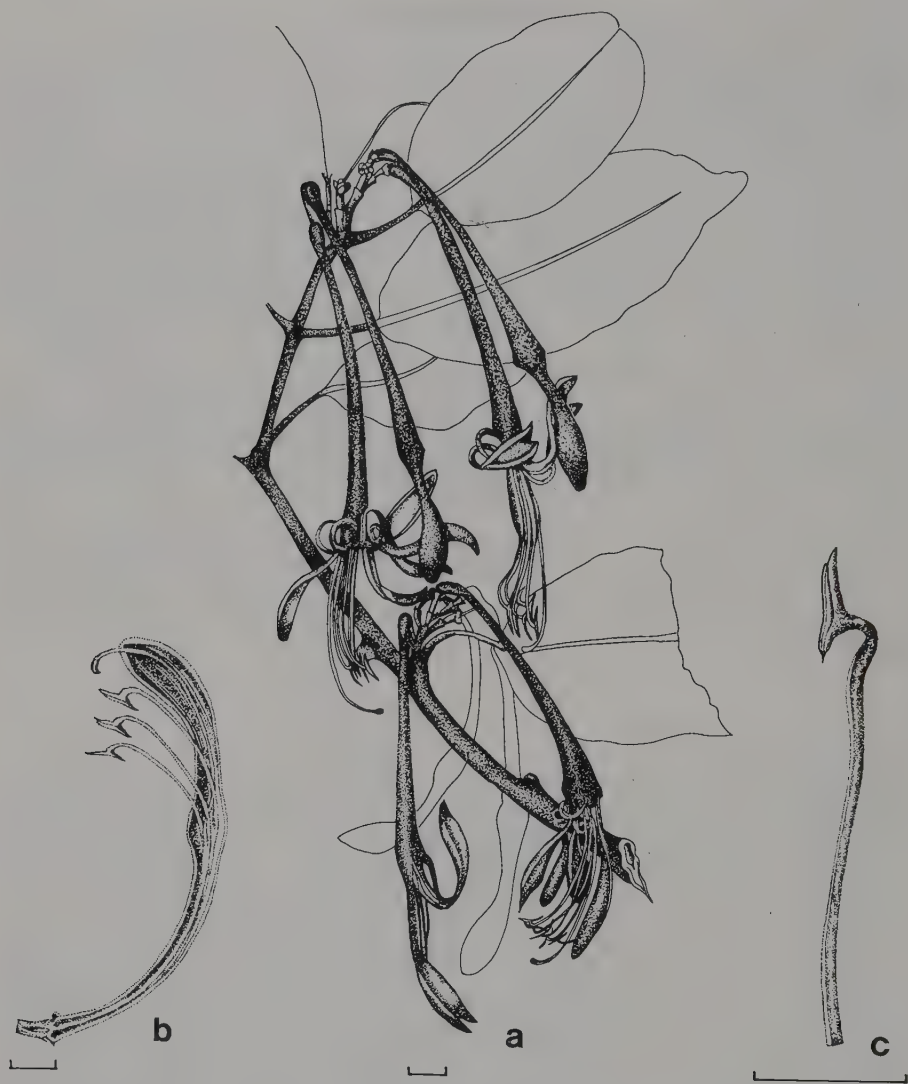


Fig. 34. *Loxanthera speciosa* Blume. a. Flower-bearing twig; b. flower in sectional view; c. upper part of stamen (Collection not cited). Redrawn from Blume (1851). Scale bars represent 1 cm.

MACROSOLEN

Macrosolen Blume in Schult. & Schult. f., Syst. Veg. 7, 2 (1830) 1731; Tiegh., Bull. Soc. Bot. France 42 (1895) 442; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 271. — Type species: *Macrosolen formosus* (Blume) Miq.

Blumella Tiegh., Bull. Soc. Bot. France 42 (1895) 441. — Type species: *Blumella loniceroides* (L.) Tiegh. [= *Macrosolen parasiticus* (L.) Danser].

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 271].

Aerial stem-parasitic shrubs, often robust, with epicortical runners bearing secondary haustoria. *Leaves* mostly opposite. *Inflorescences* axillary or inserted on the epicortical runners, a simple raceme or spike of decussate pairs of flowers, sometimes few-flowered and seemingly umbellate; bracts 3 under each flower, free or variously connate. *Corolla* 6-merous, gamopetalous, in mature bud with 6 keels or wings at the point of reflexion of the lobes, usually weakly zygomorphic but sometimes regular. *Anthers* basifixed, immobile. *Style* simple, usually with a knob-like stigma. *Fruit* ellipsoid to nearly globose. — **Fig. 35–39.**

Distribution — About 30 species in southern Asia and Malesia, extending from India to New Guinea. In *Malesia* 24 species, with the centre of diversity to the northwest, especially in Borneo.

Habitat — Humid and open forests and disturbed sites, more common in lowlands but with many species reaching altitudes of 2000–3000 m.

Ecology — In Malesia many species are aggressive, with broad host ranges, often occurring on cultivated trees.

Morphology — In some species the normally developed pairs of leaves alternate with scale leaves at intervening nodes, so that the leaves may appear to be superposed. This attribute occurs in a few species scattered in genera which are not closely related, such as *Barathranthus* and *Papuanthes* (Fig. 14), and may be a polyphyletic adaptation.

Taxonomy — Danser in *Blumea* 2 (1936) 35 revised the generic limits of *Elytranthe*, and transferred from *Elytranthe* to *Macrosolen* a few species which had earlier formed the basis of Van Tieghem's genus *Blumella*. The latter species do not occur in Malesia, but are correctly placed in *Macrosolen*, although perhaps constituting a distinct section. The two species still remaining in *Elytranthe* could possibly be accommodated in *Macrosolen* as well (see discussion under *Elytranthe*).

For discussion of taxonomic difficulty at the species level in *Macrosolen*, see Barlow, *Blumea* 40 (1995) 25–29.

KEY TO THE SPECIES

- 1a. Inflorescence of 1 or 2 pairs of flowers 2
- b. Inflorescence usually of more than 2 pairs of flowers in a raceme or spike 16
- 2a. Corolla more than 50 mm long 3
- b. Corolla 20–50 mm long 6
- c. Corolla less than 20 mm long 11
- 3a. Lateral bracts more or less connate but together not enclosing the ovary
 **12. M. formosus**
- b. Lateral bracts connate, together enclosing the ovary 4
- 4a. Stem internodes quadrangular when young; leaves usually cordate at the base, sessile **17. M. platyphyllus**
- b. Stem internodes terete from youth; leaves usually cuneate at the base, petiolate . 5
- 5a. Leaves widest below the middle; bracts not keeled **10. M. dianthus**
- b. Leaves widest above the middle; bracts keeled **8. M. crassus**

- 6a. Flowers usually subsessile; lateral bracts connate, enclosing the ovary **13. *M. geminatus***
- b. Flowers usually pedicellate, sometimes very shortly; lateral bracts free or connate but not enclosing the ovary 7
- 7a. Inflorescence normally a 2-flowered umbel 8
- b. Inflorescence normally racemose or subumbellate, sometimes reduced to 2 flowers but usually with more 9
- 8a. Lateral bracts free or nearly so, spreading; corolla in mature bud curved near the base, symmetrically winged **5. *M. bibracteolatus***
- b. Lateral bracts connate, appressed to the ovary when young; corolla in mature bud curved above the middle, asymmetrically winged **3. *M. avenis***
- 9a. Stem internodes two-edged when young; leaves usually cordate at the base and sessile **18. *M. pseudoperfoliatus***
- b. Stem internodes terete from youth; leaves cuneate or attenuate at the base, distinctly petiolate 10
- 10a. Leaves glossy above, acuminate and acute at the apex, mostly more than 5 cm long and 2 cm wide; inflorescence umbellate **21. *M. robinsonii***
- b. Leaves dull or lustrous above, mostly rounded at the apex, mostly less than 5 cm long and 2 cm wide; inflorescence racemose **11. *M. flammeus***
- 11a. Leaf lamina less than 5 cm long 12
- b. Leaf lamina mostly more than 5 cm long 14
- 12a. Corolla in mature bud crowned by a corona of dorsal appendages on the corolla lobes **9. *M. curtiflorus***
- b. Corolla in mature bud lacking a corona of dorsal appendages on the corolla lobes 13
- 13a. Leaves rounded at the apex; ovary shortly tomentose and more or less tuberculate; the distal part of the corolla weakly to strongly papillose in bud **16. *M. papillosus***
- b. Leaves acute at the apex; ovary and corolla glabrous **22. *M. surigaoensis***
- 14a. Flowers usually subsessile **13. *M. geminatus***
- b. Flowers distinctly pedicellate 15
- 15a. Leaf lamina more than 12 cm long; anther c. 5 mm long, longer than the free part of the filament **2. *M. amboinensis***
- b. Leaf lamina less than 12 cm long; anther 1.5–2 mm long, much shorter than the free part of the filament **21. *M. robinsonii***
- 16a. Corolla in mature bud more than 50 mm long 17
- b. Corolla in mature bud 28–50 mm long 20
- c. Corolla in mature bud less than 28 mm long 23
- 17a. Stem internodes quadrangular when young; leaves usually cordate at the base, subsessile **17. *M. platyphyllus***
- b. Stem internodes terete from youth; leaves usually cuneate at the base, petiolate 18
- 18a. Leaf lamina more than 20 cm long, subsessile, bullate between the main veins; floral bracts 3–5 mm long **1. *M. acunae***

- b. Leaf lamina mostly less than 20 cm long, mostly cuneate at the base and distinctly petiolate, smooth; floral bracts 1–3 mm long 19
- 19a. Inflorescence of 1–4 pairs of flowers; axis 5–17 mm long, not subtended at the base by an involucre of short broadly triangular bracts; pedicels spreading, 3–7 mm long; bracts rounded, 1–2 mm long **12. *M. formosus***
- b. Inflorescence of 2–7 pairs of flowers; axis 10–20 mm long, subtended at the base by an involucre of short broadly triangular bracts; pedicels appressed to the axis, 1–4 mm long; bracts keeled, acute, 2–3 mm long **24. *M. x tubiflorus***
- 20a. Leaf lamina more than 15 cm long; free part of filament about 4 times as long as anther **4. *M. beccarii***
- b. Leaf lamina mostly less than 12 cm long; free part of filament 1.5–2 times as long as the anther 21
- 21a. Stem internodes angular when young; leaves mostly cordate at the base and sessile; corolla more than 35 mm long **18. *M. pseudoperfoliatus***
- b. Stem internodes terete from youth; leaves mostly cuneate to truncate at the base and petiolate; corolla less than 35 mm long 22
- 22a. Leaf lamina usually dull on both surfaces, rounded at the apex, attenuate at the base to a winged petiole **20. *M. retusus***
- b. Leaf lamina glossy above, dull below, acuminate and mostly acute at the apex, shortly cuneate to truncate at the base to a sharply defined petiole **15. *M. melintangensis***
- 23a. Leaf lamina more than 15 cm long; petiole mostly more than 15 mm long; free part of filament 3–5 times as long as the anther **14. *M. macrophyllus***
- b. Leaf lamina mostly less than 15 cm long; petiole mostly less than 15 mm long; free part of filament 1–3 times as long as the anther 24
- 24a. Corolla tube more than 12 mm long 25
- b. Corolla tube mostly less than 10 mm long 26
- 25a. Leaf lamina usually dull on both surfaces, rounded at the apex, attenuate at the base to a winged petiole **20. *M. retusus***
- b. Leaf lamina glossy above, dull below, acuminate and mostly acute at the apex, shortly cuneate to truncate at the base to a sharply defined petiole **15. *M. melintangensis***
- 26a. Leaf lamina less than 6 cm long; the corolla about 7 mm long **19. *M. pusillus***
- b. Leaf lamina mostly more than 6 cm long; the corolla more than 8 mm long ... 27
- 27a. Stem internodes quadrangular when young; leaf lamina thick, mostly sessile, mostly rounded towards the apex **23. *M. tetragonus***
- b. Stem internodes terete from youth; leaf lamina coriaceous, distinctly petiolate, mostly attenuate or acuminate towards the apex 28
- 28a. Corolla tube mostly red, about one fourth the corolla length; anther 2–3.5 mm long **6. *M. brevītubus***
- b. Corolla tube mostly yellow or green, about one half the corolla length; anther 0.5–2 mm long **7. *M. cochinchinensis***

1. *Macrosolen acunae* (Merr.) Danser

Macrosolen acunae (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 343. — *Elytranthe acunae* Merr., Philipp. J. Sc., Bot. 13 (1918) 279. — Type: *Acuna* FB 23386, lecto, see note 2, Mindanao, Lanao.

Macrosolen nobilis Danser, Rec. Trav. Bot. Néerl. 31 (1934) 240. — Type: *Richards* 1403, Sarawak, Mt Dulit.

Glabrous. *Leaves* opposite, sometimes seemingly superposed; lamina ovate, 20–30 (–50) by 7–10 (–19) cm, truncate to cordate at the base, subsessile or with a petiole to 2 mm long, often bullate between the veins, acuminate and acute at the apex, lustrous above, dull below; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes and on the epicortical runners, a raceme of 2–6 opposite crowded pairs of flowers; axis 5–10 mm long, subtended at the base by an involucre of broad short bracts; pedicels 1–2 mm long; bracts erect, acuminate, 3–5 mm long. *Corolla* in mature bud 6-merous, 50–85 mm long, slender in the lower part, clavate, winged and acute at the apex, red or orange below and yellow or greenish above; tube in the open flower 28–60 mm long with the narrowly spatulate lobes reflexed 5–7 mm higher. *Anther* 4–5 mm long, saggitate at the base, subacute; free part of the filament about twice as long, gradually widened upwards. — **Fig. 38a.**

Distribution — *Malesia*: Peninsular Malaysia, northern Borneo, Mindanao.

Habitat & Ecology — 150–600 m altitude; the only recorded host is *Koiloclepa*.

Notes — 1. Similar vegetatively to *Macrosolen beccarii*, differing in the longer corolla with different proportions, especially at the apex.

2. The holotype of *Elytranthe acunae* (PNH) is not extant. An isotype has been seen (US) and designated lectotype of the species name.

2. *Macrosolen amboinensis* (Merr.) Danser

Macrosolen amboinensis (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 343. — *Elytranthe amboinensis* Merr., Interpr. Rumph. Herb. Amb. (1917) 206. — Type: *Robinson* 515, Moluccas, Ambon.

Glabrous. *Leaves* opposite; lamina ovate, 12–23 by 4–10 cm, cuneate to truncate at the base to a petiole 8–15 mm long, acuminate and acute at the apex, glossy above, dull below; venation pinnate with the midrib raised below and the major veins distinct above. *Inflorescences* at the nodes, an umbellate raceme of 1 or 2 opposite pairs of flowers; axis 4–7 mm long; pedicels 2–4 mm long; central bract c. 1.5 mm long, acute; lateral bracts slightly shorter, usually connate to near the apex. *Corolla* in mature bud 6-merous, 15–20 mm long, strongly winged and inflated to near the middle, cylindrical above, obtuse at the apex, green or red below, dark coloured in the middle and green above; tube in the open flower 4–6 mm long, campanulate, the lobes fully reflexed 3–5 mm higher. *Anther* c. 5 mm long, obtuse, slightly longer than the free part of the filament.

Distribution — *Malesia*: Moluccas (Ambon, Ceram).

Habitat & Ecology — Lowlands; no host recorded.

Note — Related to *Macrosolen geminatus*, differing in distinctly pedicellate flowers and more robust habit.

3. *Macrosolen avenis* (Blume) Danser

Macrosolen avenis (Blume) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 343; Backer & Bakh. f., Fl. Java 2 (1965) 70. — *Loranthus avenis* Blume, Verh. Bat. Genootsch. 9 (1823) 190. — Type: *Blume s.n.*, Java.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 275].

Glabrous. *Leaves* opposite; lamina narrowly ovate to ovate, 4–10(–13) by 1.5–4(–6) cm wide, cuneate to truncate at the base to a petiole 2–6 mm long, usually acuminate and acute or obtuse at the apex, lustrous above, dull below; venation pinnate with the midrib distinct above and prominent below and the main laterals usually obscure on both sides. *Inflorescences* at the nodes, an umbel of usually 1 opposite pair of flowers; axis 0.5–6 mm long; pedicels 2–6 mm long; bracts triangular, acute, c. 1.5 mm long, connate only at the base and spreading as a shallow dish. *Corolla* in mature bud 6-merous, 30–40 mm long, slender, weakly and unequally winged near the middle, usually curved in the upper part and weakly clavate and acute or obtuse at the apex, mostly red or rarely yellow or green, sometimes violet above; tube in the open flower 20–28 mm long, split more deeply on the concave side, with the lobes reflexed 3–4 mm higher. *Anther* c. 2 mm long, acute, about half as long as the free part of the filament.

Distribution — Thailand to Vietnam; *Malesia*: Sumatra, Peninsular Malaysia, Java.

Habitat & Ecology — Mostly in highlands from 1700 to 2600 m altitude, less frequently down to 250 m in Indochina; the only recorded hosts are *Ardisia* and *Vaccinium*.

Note — Similar to *Macrosolen bibracteolatus*, differing in the bract and corolla characters described in the key. The species are sympatric only in eastern Indochina and northern Sumatra. Some specimens from these areas are difficult to discriminate, suggesting limited introgression.

4. *Macrosolen beccarii* Becc.

Macrosolen beccarii Tiegh. ex Becc., For. Born. (1902) 518. — Type: *Beccari 610*, Sarawak.

Macrosolen borneanus Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 278. — Type: *Amdjah 329*, Kalimantan, 'Oeloe Tjihan'.

Glabrous. *Leaves* opposite, often apparently superposed; lamina ovate, 15–28(–37) by 5–13 cm, truncate to cordate at the base, subsessile or with a petiole to 4 mm long, acuminate and acute at the apex, glossy or lustrous above, dull below; venation pinnate with the midrib and the main laterals distinct on both sides and the reticulum often visible above. *Inflorescences* at the nodes, a raceme of 2–6(–8) opposite crowded pairs of flowers; axis 9–14 mm long, usually subtended at the base by an involucre of broad short bracts; pedicels c. 2 mm long; floral bracts erect, acuminate, c. 2 mm long. *Corolla* in mature bud 6-merous, 30–40 mm long, moderately robust, cylindric below, abruptly widened, clavate, strongly winged and obtuse at the apex, mostly red below and black above; tube in the open flower 15–20 mm long with the spatulate marginate lobes reflexed 5–8 mm higher. *Anther* 2–3 mm long, shortly saggitate at the base, acute; free part of the filament about four times as long, usually gradually widened upwards. —

Fig. 36 d–f.

Distribution — *Malesia*: Borneo.

Habitat & Ecology — Lowlands; the only recorded host is *Cephalomappa*.

Note — For comparison with *Macrosolen acunae*, see there.

5. *Macrosolen bibracteolatus* (Hance) Danser

Macrosolen bibracteolatus (Hance) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 343. — *Loranthus bibracteolatus* Hance, J. Bot. 18 (1880) 301. — Type: *Hance 20792 (ex Gerlach)*, not seen.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 9].

Glabrous. *Leaves* opposite; lamina narrowly ovate to ovate, mostly 8–12 cm long, 2–6 cm wide, cuneate at the base to a petiole 1–3 mm long, acuminate and acute or obtuse at the apex, glossy above, dull below; venation pinnate with the midrib and the main laterals distinct above and the midrib prominent below. *Inflorescences* at the nodes, an umbel of 1 opposite pair of flowers; axis 1–4 mm long; pedicels 1–4 mm long; bracts 0.8–1.5 mm long, concave, somewhat appressed at the bud stage, the laterals ones connate. *Corolla* in mature bud 6-merous, 25–35 mm long, often curved near the base, gradually widened upwards, winged in the upper part, clavate and obtuse at the apex, pink or red, sometimes yellow or green above; tube in the open flower 16–24 mm long with the lobes reflexed or twisted slightly higher. *Anther* c. 4 mm long, obtuse, equal to or shorter than the free part of the filament.

Distribution — Southern China (including Hainan) and Vietnam; *Malesia*: Sumatra, Borneo. The area of the species may be disjunct.

Habitat & Ecology — Mostly in highlands from 1800 to 3000 m altitude, less frequently down to 700 m; no hosts recorded.

Note — Similar to *Macrosolen avenis*; see there for comparison.

6. *Macrosolen brevitubus* Barlow

Macrosolen brevitubus Barlow, Blumea 40 (1995) 25. — Type: *Chew 980*, Sarawak, Marudi.

Glabrous. *Leaves* opposite; lamina narrowly ovate to elliptic, 8–13 by 2.5–5 cm, shortly cuneate to truncate at the base to a petiole 1–4 mm long, attenuate to acuminate and shortly rounded to acute at apex, lustrous or dull above, dull and paler below; venation pinnate with midrib and main laterals visible above and the midrib prominent below; lamina in juvenile state linear, to 15 cm long, 0.5–1 cm wide, otherwise similar to adult leaves. *Inflorescence* a raceme of 4 or 5 opposite pairs of flowers; axis 8–15 mm long; pedicels 1–3 mm long. *Corolla* in mature bud 6-merous, 15–25 mm long, inflated in the lower part, winged below the middle, weakly clavate above a long neck and acute at apex, mostly red with one or two black bands at neck and apex; tube in the open flower 4–6 mm long with the narrowly spatulate lobes reflexed 3–5 mm higher. *Anther* 2–3.5 mm long, obtuse, about half to three fourths as long as the free part of the filament.

Distribution — *Malesia*: Borneo.

Habitat & Ecology — Lowland dipterocarp forest to 300 m altitude; the only recorded host is *Strombosia*.

Note — Related to *M. macrophyllus*; for distinction as a species see Barlow, l.c.



Fig. 35. *Macrosolen cochinchinensis* (Lour.) Tiegh. Borneo, NW Kalimantan, Sanggau. Photo A. Else-ner, 1961.

7. *Macrosolen cochinchinensis* (Lour.) Tiegh.

Macrosolen cochinchinensis (Lour.) Tiegh., Bull. Soc. Bot. France 41 (1894) 122; Backer & Bakh. f., Fl. Java 2 (1965) 69. — *Loranthus cochinchinensis* Lour., Fl. Coch. (1790) 195. — Type: not located.

[For extensive additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 279; 16 (1938) 5; Philipp. J. Sc. 58 (1935) 43].

Glabrous or rarely the inflorescence shortly pale-tomentose. *Leaves* opposite or scattered, the normally developed ones sometimes alternating with cataphylls; lamina narrowly to broadly elliptic or ovate, 4–16 by 2–7 cm, cuneate to truncate at the base to a petiole (1–)3–10 mm long; usually acuminate and acute but sometimes obtuse or shortly rounded at the apex, lustrous above, dull below; venation pinnate with the midrib prominent and the main laterals faintly visible on both sides. *Inflorescences* at the nodes, a sometimes subumbellate or spicate raceme of 2–7 opposite pairs of flowers; axis slender, 5–20(–40) mm long, subtended at the base by an involucre of 1 or 2 pairs of small broadly triangular bracts; pedicels slender, 0–6 mm long. *Corolla* in mature bud 6-merous, 8–18(–23) mm long, gradually widened or slightly inflated upwards, weakly winged near the middle, angular, clavate and obtuse or rarely acute at the apex, mostly yellow or green or rarely pink or red below, dark-coloured at the neck and yellow or red above; tube in the open flower 5–10(–14) mm long with the lobes reflexed slightly higher. *Anther* 0.5–2 mm long, acute, about half to one third as long as the free part of the filament. — **Fig. 35.**

Distribution — Southern Asia from the Himalayas eastwards to southern China and Indochina; *Malesia*: common and widespread from Peninsular Malaysia to New Guinea (Bird's Head Peninsula).

Habitat & Ecology — Humid and open forests and disturbed sites; very common in lowlands but occasionally reaching as high as 2270 m altitude; recorded hosts many.

Note — Barlow in Austral. J. Bot. 22 (1974) included in *Macrosolen cochinchinensis* all New Guinean specimens previously referred to *M. suberosus*. The latter name is now treated as conspecific with *M. geminatus* (see note there).

8. *Macrosolen crassus* Danser

Macrosolen crassus Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 285. — Type: Endert 3552, Kalimantan, 'Kong Kemoel'.

Glabrous. *Leaves* opposite; lamina elliptic to oblong, widest above the middle, 6–13 by 2–4 cm, attenuate at the base to an obscure petiole 5–10 mm long, rounded at the apex, dull on both sides; venation pinnate with only the midrib visible above and prominent below. *Inflorescences* at the nodes, robust, mostly an umbel of 1 opposite pair of flowers, sometimes with the axis prolonged and rarely bearing a second pair of flowers; axis 3–10 mm long; pedicels 1.5–3 mm long, central bract keeled, 4–6 mm long; lateral bracts keeled, connate, together enclosing the ovary. *Corolla* in mature bud 6-merous, 70–110 mm long, robust, widened upwards, angular above, clavate and rounded at the apex, red; tube in the open flower 60–90 mm long with the lobes reflexed slightly

higher. *Anther* 8–10 mm long, obtuse, about two thirds as long as the free part of the filament. — **Fig. 38b.**

Distribution — *Malesia*: Sumatra, Borneo.

Habitat & Ecology — 80–540 m altitude; the only recorded host is *Casuarina*.

9. *Macrosolen curtiflorus* (Elmer) Danser

Macrosolen curtiflorus (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 344. — *Loranthus curtiflorus* Elmer, Leaflet. Philipp. Bot. 6 (1913) 1964. — Type: *Elmer 14089*, Mindanao, Cabadbaran.

Glabrous. Stem internodes more or less flattened quadrangular upwards when young. *Leaves* opposite; lamina elliptic, mostly 3–5 cm long, mostly 1.5–3 cm wide, shortly cuneate at the base to a petiole 5–8 mm long, obtuse or rounded at the apex, dull on both sides; venation pinnate with the midrib prominent and the main laterals visible on both sides. *Inflorescences* at the nodes, a subumbellate raceme of 2 opposite pairs of flowers; axis 6–10 mm long; pedicels 2–3 mm long. *Corolla* in mature bud 6-merous, c. 15 mm long, slightly inflated, 6-angular above the middle, with a crown at the apex formed from dorsal appendages on the segments; tube in the open flower c. 7 mm long. *Anther* c. 3 mm long.

Distribution — *Malesia*: Philippines (Mindanao).

Habitat & Ecology — 1800 m altitude; no host recorded.

Note — The species is known only from the type (PNH), which is no longer extant. If the diagnostic characters are correct, the species is singular in the genus in having a corona at the tip of the corolla bud. The conservation status of the species requires consideration.

10. *Macrosolen dianthus* (King) Danser

Macrosolen dianthus (King) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 344. — *Loranthus dianthus* King, J. As. Soc. Beng. 56, ii (1887) 96. — Type: *Scortechini 604a*, lecto, see note 2, Perak. *Loranthus subsessilis* Merr., Philipp. J. Sc., Bot. 7 (1912) 263. — *Macrosolen subsessilis* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 345. — Type: *Merrill 8315*, lecto, see note 2, Mindanao, Sax River.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 287; 16 (1938) 13].

Glabrous. *Leaves* opposite; lamina (in the Malesian region) narrowly ovate to ovate, 9–15 by 2.5–7 cm, shortly cuneate to truncate at the base to a petiole 2–8 mm long, acuminate and acute at the apex, dull on both sides; venation pinnate with the midrib prominent below and the main veins distinct on both sides. *Inflorescences* at the nodes, a pseudo-umbel of 1 opposite pair of subsessile flowers; axis 1–3 mm long; pedicels 0–1 mm long; central bract orbicular, 2–3 mm long; lateral bracts 2–3 mm long, connate, together almost completely enclosing the ovary. *Corolla* in mature bud 6-merous, 55–85 mm long, winged at about two thirds the length, clavate and often minutely mucronate at the apex, red or green below, often green at the neck and red above; tube in the open flower 40–60 mm long with the lobes reflexed slightly higher. *Anther* 5–8 mm long, obtuse, equal to or shorter than the free part of the filament.

Distribution — Vietnam; *Malesia*: Peninsular Malaysia, Mindanao. The species area appears to be disjunct.

Habitat & Ecology — 100–600 m altitude; no hosts recorded.

Notes — 1. Closely related to *Macrosolen platyphyllus*; for differences see there. Specimens in Peninsular Malaysia and Indochina with leaves truncate to cordate at the base and rounded at the apex, referred to *M. krempfii* by previous authors, are possibly intergrades between *M. dianthus* and *M. platyphyllus*.

2. In the protologue of *Loranthus dianthus* King cited four collections, which are therefore syntypes. *Scortechini 604a*, seen by King and bearing an analysis by Gamble, is selected as lectotype of the species name. The holotype of *Loranthus subsessilis* (PNH) is no longer extant. Isotypes have been seen (US 901951, L); the former is more substantial and is designated lectotype of the species name.

11. *Macrosolen flammeus* Danser

Macrosolen flammeus Danser, Rec. Trav. Bot. Néerl. 31 (1934) 230. — Type: *Clemens 29807*, Sabah, Mt Kinabalu.

Glabrous except for the corolla rarely shortly tomentose. *Leaves* opposite; lamina narrowly ovate to narrowly obovate, 3–5.5 by 1.2–2 cm, cuneate to attenuate at the base to a petiole 2–5 mm long, recurved at the margin, mostly rounded and shortly mucronate or rarely acute at the apex, dull or slightly lustrous above, dull below; venation pinnate with the midrib distinct above and raised below and the main laterals visible on both sides. *Inflorescences* at the nodes, a raceme of 1 or 2 opposite pairs of flowers; axis 2–7 (–13) mm long; pedicels 1–6 mm long; bracts small, the lateral ones usually connate. *Corolla* in mature bud 6-merous, 22–28 mm long, slender, angular, weakly alate above the middle, weakly clavate and acute at the apex, mostly red or pink below, dark coloured at the neck and green to yellow above; tube in the open flower 12–18 mm long with the lobes reflexed 3–4 mm higher. *Anther* 1.5–2 mm long, acute, about one fourth as long as the free part of the filament. — **Fig. 36a.**

Distribution — *Malesia*: Borneo.

Habitat & Ecology — Known mostly from Mt Kinabalu from 2400 to 3000 m altitude but recorded down to sea level; recorded hosts include *Phyllocladus* and *Tristania*.

12. *Macrosolen formosus* (Blume) Miq.

Macrosolen formosus (Blume) Miq., Fl. Ind. Bat. 1 (1856) 27; Baçker & Bakh. f., Fl. Java 2 (1965) 69.

— *Loranthus formosus* Blume, Bijdr. (1825) 664. — Type: *Blume s.n.*, Java.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 287].

Glabrous. *Leaves* opposite; lamina narrowly ovate to ovate, 10–16(–30) by 5–13 cm, cuneate at the base to a petiole 4–12 mm long (in Peninsular Malaysian specimens sometimes truncate or cordate at the base and subsessile), acuminate and acute at the apex, slightly lustrous above, dull below; venation pinnate with the midrib and the main laterals distinct on both sides. *Inflorescences* at the nodes and sometimes along the internodes and on the epicortical runners, a raceme (sometimes subumbellate or umbellate)



Fig. 36. *Macrosolen flammeus* Danser. a. Flower-bearing twig. — *M. melintangensis* (Korth.) Miq. b. Flower-bearing twig; c. inflorescence. — *M. beccarii* Becc. d. Part of stem with fruiting inflorescence; e. flower bud; f. flower (a: Clemens 29807; b: Ramos & Chan BS 30447; c: Endert 3999; d: Amdjah 329; e, f: Haviland =478). a Redrawn from Danser (1934), b redrawn from Danser (1935), c–f redrawn from Danser (1931). Scale bars represent 1 cm.

of 1–4 opposite pairs of flowers; axis 5–17 mm long; pedicels 3–7 mm long; bracts 1–2 mm long, rounded, the laterals sometimes connate. Corolla in mature bud 6-merous, 60–100 mm long, gradually widened upwards, moderately winged below the neck, cla-

vate, ribbed and rounded at the apex, mostly red or rarely yellow below and often striped green or darker red and white or cream above; tube in the open flower 45–75 mm long with the lobes reflexed or 5–7 mm higher. *Anther* 5–7 mm long, weakly sagittate at the base, acute, slightly shorter than the free part of the filament. — **Fig. 38e.**

Distribution — *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java.

Habitat & Ecology — Humid forests, mostly 800–1650 m altitude, less frequently down to 150 m; recorded hosts include *Diospyros* and *Ficus*.

Note — Peninsular Malaysian specimens with large subsessile cordate leaves may be the result of introgression from species such as *Macrosolen acunae*.

13. *Macrosolen geminatus* (Merr.) Danser

Macrosolen geminatus (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 344. — *Loranthus geminatus* Merr., Philipp. J. Sc., Bot. 4 (1909) 146. — Type: Merrill 5444, lecto, see note 2, Mindanao.

Loranthus mcgregorii Merr., Philipp. J. Sc., Bot. 4 (1909) 146. — *Macrosolen mcgregorii* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 345. — Type: McGregor BS 1266, lecto, see note 2, Bohol.

Loranthus angulatus Elmer, Leaflet Philipp. Bot. 3 (1911) 1074. — *Macrosolen angulatus* (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 343. — Type: Elmer 10804, lecto, see note 2, Sibuyan, Mt Giting-Giting.

Elytranthe suberosa Lauterb., Nova Guinea 8 (1912) 816. — *Macrosolen suberosus* (Lauterb.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 345. — Type: Gjellerup 148, lecto, Irian Jaya, 'Hollandia'.

Loranthus worcesteri Merr., Philipp. J. Sc., Bot. 9 (1914) 284. — *Macrosolen worcesteri* (Merr.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 346. — Type: Fenix BS 15673, see note 2, Mindanao.

Macrosolen coriaceus Danser, Blumea 2 (1936) 37. — Type: Kaudern 507, Celebes, Banggai.

Macrosolen cochinchinensis (Lour.) Tiegh. var. *lanceolatus* Barlow, Austral. J. Bot. 22 (1974) 556. — Type: Womersley & Millar NGF 7755, Papua New Guinea, near Karap.

[For additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 554 (excl. *Loranthus cochinchinensis*)].

Glabrous, rarely somewhat glaucous. *Leaves* opposite; lamina usually elliptic or ovate, sometimes lanceolate, (4–)6–12(–16) by (1–)3–8 cm, cuneate to truncate at the base to a petiole 0–10(–15) mm long (i.e., rarely sessile), variable at the apex from acuminate and acute to bluntly obtuse or rounded, dull or glossy above, usually dull below; venation pinnate with the midrib prominent below and the larger veins distinct above. *Inflorescences* at the nodes, normally a spike of 1 or 2 or rarely 3 opposite subcapitate pairs of flowers; axis 3–8(–12) mm long, sometimes with an involucre of 1–3 pairs of small bracts at or near the base; pedicels vestigial or very rarely up to 2 mm long; central bract usually acute, 1.5–2 mm long; lateral bracts slightly shorter, usually connate to near the apex and enclosing the ovary. *Corolla* in mature bud 6-merous, 9–16(–23) mm long, strongly winged and inflated to near the middle, cylindrical above, obtuse at the apex, mostly yellow or red below, dark coloured in the middle and green or yellow above; tube in the open flower 3–8(–12) mm long, campanulate, with the lobes fully reflexed slightly higher. *Anther* 1–3.5 mm long, obtuse, longer or shorter than the free part of the filament. — **Fig. 37c, d.**

Distribution — *Malesia*: Philippines (southern part), Celebes, New Guinea.

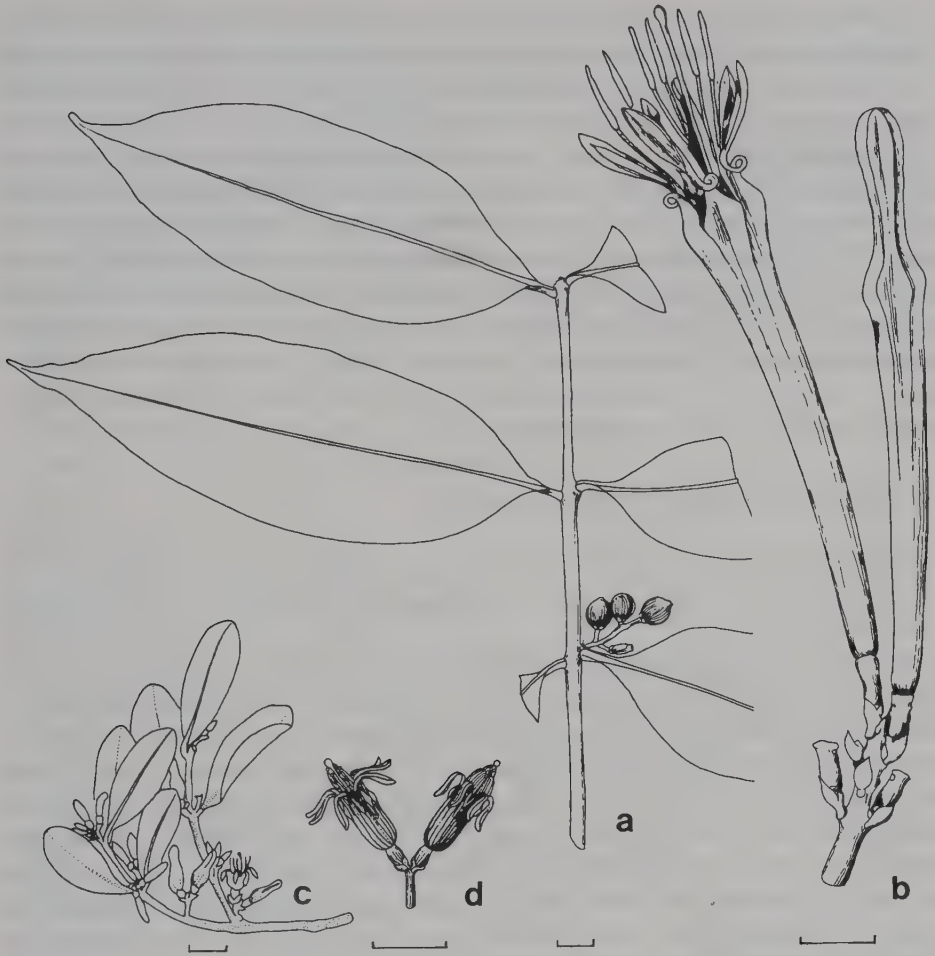


Fig. 37. *Macrosolen* \times *tubiflorus* (Ridl.) Danser. a. Part of stem with fruiting inflorescence; b. inflorescence. — *M. geminatus* (Merr.) Danser. c. Flower-bearing twig; d. inflorescence (a – c: not cited; d: *Doctors van Leeuwen 10006*). a, b Redrawn from Danser (1934), c redrawn from Barlow (1981), d redrawn from Danser (1931). Scale bars represent 1 cm.

Habitat & Ecology — Mostly in closed humid forests, 0–2300 m altitude; recorded hosts include *Alstonia*, *Castanopsis*, *Grewia*, *Nothofagus*, *Opocunonia*, and *Pittosporum*.

Notes — 1. There is no consistent basis on which *Macrosolen geminatus*, *M. angulatus*, *M. mcgregorii*, *M. worcesteri*, *M. suberosus*, *M. coriaceus* and *M. cochinchinensis* var. *lanceolatus* can be distinguished, and they are accordingly treated together as a single relatively polymorphic species. There is evidence of local race differentiation, especially in New Guinea and Celebes, mainly involving leaf shape and texture.

2. Barlow [1974, and in Handb. Fl. Papua New Guinea 2 (1981) 247] treated the New Guinean specimens of *M. suberosus* (= *M. geminatus*) as conspecific with *M. cochinchinensis*. True *M. cochinchinensis* occurs in New Guinea only in the Bird's Head Peninsula.

3. The holotype of *L. geminatus* (PNH) is no longer extant. Isotypes have been seen (US 710732, NY); the former is more substantial and is designated lectotype of the species name. The holotype of *L. mcgregorii* (PNH) is no longer extant. Isotypes have been seen (NY, US 439241); the former is more substantial and is designated lectotype of the species name. The holotype of *L. angulatus* (PNH) is no longer extant. Isotypes have been seen (NY, US 779402); the former is more substantial and is designated lectotype of the species name. The holotype of *L. worcesteri* (PNH) is no longer extant. A fragmentary isotype has been seen (US) but has not been designated lectotype of the species name, pending a search for a better specimen.

14. *Macrosolen macrophyllus* (Korth.) Miq.

Macrosolen macrophyllus (Korth.) Miq., Fl. Ind. Bat. 1 (1856) 829. — *Loranthus macrophyllus* Korth., Verh. Bat. Genootsch. 17 (1839) 280. — Type: *Korthals* 283, Sumatra, Mt Malintang.
Macrosolen curvinervis Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 286. — Type: *Endert* 2556, Kalimantan, 'Long Hoet'.

Glabrous. *Leaves* opposite; lamina broadly ovate, 15–28 by 8–15 cm, truncate to weakly cordate at the base to a petiole (5–)15–22 mm long, thick, obtuse or rounded or rarely shortly acuminate and acute at the apex, glossy above, dull or lustrous below; venation pinnate with the midrib and the strongly incurved main laterals distinct above and prominent below. *Inflorescences* at the nodes, a raceme of 3–6 opposite pairs of flowers; axis 15–25 mm long, slender; pedicels 2–4 mm long. *Corolla* in mature bud 6-merous, 20–25 mm long, inflated below, contracted to a slender neck, clavate, angular and acute at the apex, red below, black at the neck and green above; tube in the open flower 4–7 mm long with the lobes reflexed 4–6 mm higher. *Anther* c. 2 mm long, acute, one third to one fifth as long as the free part of the filament.

Distribution — *Malesia*: Sumatra, Borneo.

Habitat & Ecology — Lowlands to 1075 m altitude; no hosts recorded.

15. *Macrosolen melintangensis* (Korth.) Miq.

Macrosolen melintangensis (Korth.) Miq., Fl. Ind. Bat. 1, 1 (1856) 830. — *Loranthus melintangensis* Korth., Verh. Bat. Genootsch. 17 (1839) 281. — Type: *Korthals* s.n., Sumatra, Mt Malintang.
Macrosolen javanus Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 289; Backer & Bakh. f., Fl. Java 2 (1965) 70. — Type: *Docters van Leeuwen* 3024, Java, Mt Guntur.
 [For extensive additional synonymy see Barlow, *Blumea* 40 (1995) 26].

Glabrous except for the inflorescence very rarely papillose hairy. *Leaves* opposite; lamina more or less ovate, (5–)8–12(–18) by 1.5–6 cm, shortly cuneate to truncate or very rarely cordate at the base to a petiole (3–)6–15(–18) mm long, usually slightly to strongly acuminate and acute at the apex but sometimes finally rounded, shining or glossy above, dull and paler below; venation pinnate, visible on the upper surface, with

only the midrib raised, dark coloured and visible below. *Inflorescences* at the nodes, a short sometimes subumbellate raceme of 2–4 opposite pairs of flowers; axis usually slender, 3–10(–16) mm long (or slightly longer in fruit), often subtended at the base by an involucre of a few acuminate prophylls; pedicels slender, (1–)2–4 mm long (to 5 mm in fruit). *Corolla* in mature bud 6-merous, (15–)20–30(–35) mm long, usually slender, slightly inflated and weakly 6-ribbed or 6-winged at or above the middle, clavate, angular and usually acute at the apex, mostly pink or red or orange, with a dark band at the neck and grading to yellow or green above; tube in the open flower mostly 12–18 mm long with the lobes reflexed 2–3 mm higher. *Anther* 1.5–3 mm long, about two thirds as long as the free part of the filament. — **Fig. 36b, c.**

Distribution — Thailand, Indochina; *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java, Philippines.

Habitat & Ecology — Common, mostly in highlands from 1000 to 2350 m altitude, less frequently down to sea level; the only recorded host is *Ficus*.

Note — For a discussion of circumscription as a species, see Barlow, *Blumea* 40 (1995) 26–29.

16. *Macrosolen papillosus* (Gamble) Danser

Macrosolen papillosus (Gamble) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 345. — *Elytranthe papillosa* Gamble, Kew Bull. 1913 (1913) 45. — Type: *Ridley 2045*, Singapore, Kranji.

Glabrous except for the ovary shortly tomentose and more or less tuberculate and the distal part of the corolla weakly to strongly papillose in bud. *Leaves* opposite; lamina narrowly obovate to spatulate, 3–4 by 1–2 cm, attenuate at the base to a petiole 1–3 mm long, rounded at the apex, dull on both sides; venation almost curvined with the midrib and the main laterals visible above and only the midrib prominent below. *Inflorescences* at the nodes, an umbel of 1 pair of flowers, sometimes extended as a raceme of 2 pairs of flowers; axis 1.5–6 mm long; pedicels 1–2 mm long; bracts small, the lateral ones usually connate. *Corolla* in mature bud 6-merous, 10–15 mm long, widened upwards to 6 tooth-like wings in the middle, clavate and obtuse or rounded at the apex, yellow or green; tube in the open flower 5–8 mm long with the lobes reflexed 2–3 mm higher. *Anther* c. 1 mm long, obtuse, about half as long as the free part of the filament.

Distribution — *Malesia*: Peninsular Malaysia, Singapore, Borneo (Sarawak).

Habitat & Ecology — 0–1000 m altitude; no hosts recorded.

Note — Similar to *Macrosolen flammeus*, differing in shorter corollas with more distinct tooth-like wings, verrucose inflorescence parts and papillose fruits.

17. *Macrosolen platyphyllus* (King) Danser

Macrosolen platyphyllus (King) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 345. — *Loranthus platyphyllus* King, J. As. Soc. Beng. 56, ii (1887) 97. — Type: *Scortechini ?606*, Perak.

Macrosolen latifolius Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 291. — Type: *Haviland 2183*, lecto, see note 2, Sarawak, Kuching.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 294].

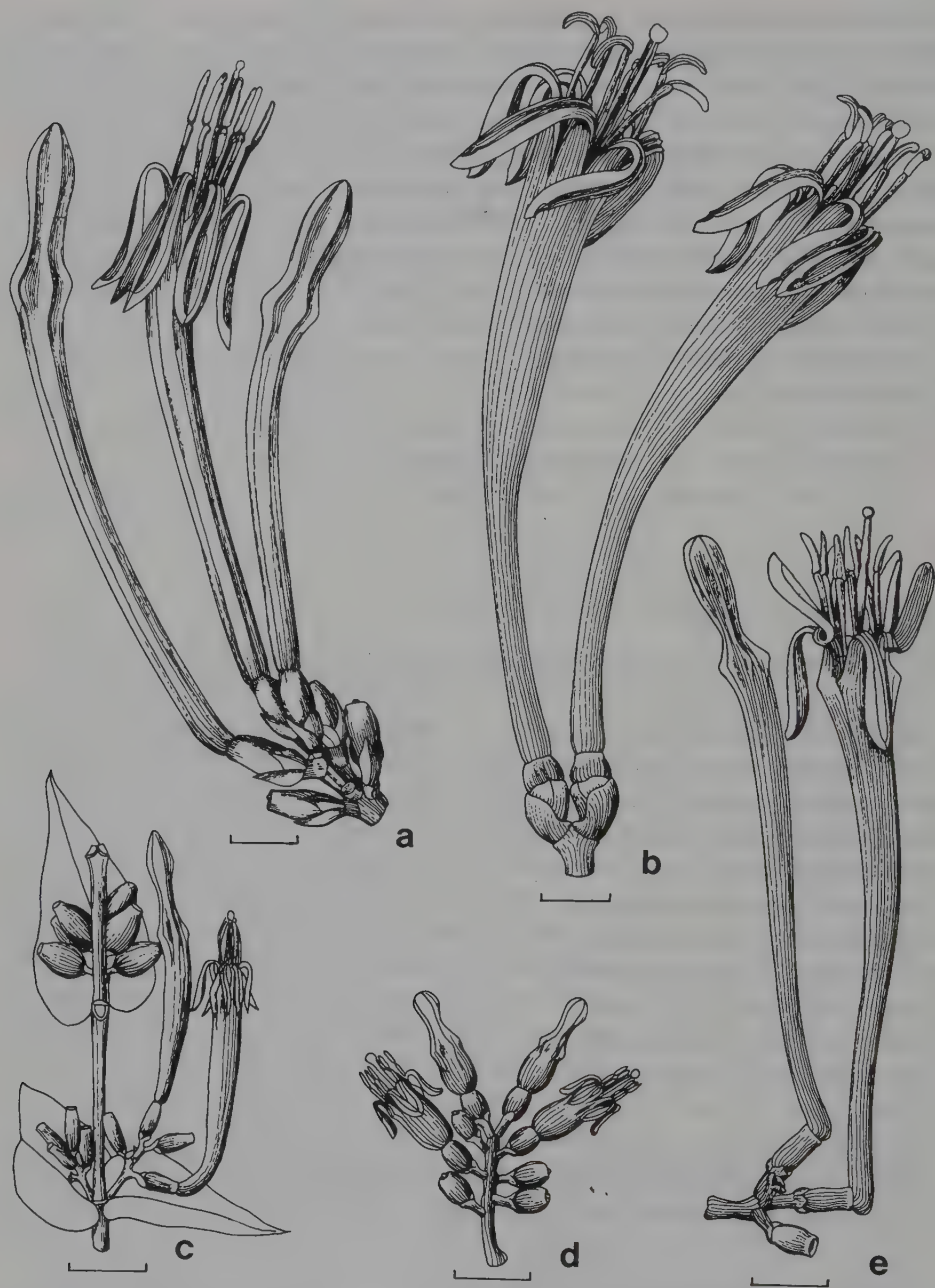


Fig. 38. *Macrosolen acunae* (Merr.) Danser. a. Inflorescence. — *M. crassus* Danser. b. Inflorescence. — *M. pseudoperfoliatus* (Zoll.) Miq. c. Part of stem with flowering and fruiting inflorescences. — *M. tetragonus* (Blume) Miq. d. Inflorescence. — *M. formosus* (Blume) Miq. e. Inflorescence (a: Richards 1403; b: Endert 3552; c: *Ultée* s. n.; d: Danser 6675; e: *Bakhuizen van den Brink* 5130). a Redrawn from Danser (1934), b–e redrawn from Danser (1931). Scale bars represent 1 cm.

Glabrous. Stem internodes distinctly quadrangular when young. *Leaves* opposite; lamina broadly ovate to cordate-orbicular, 7–19 by 5–13 cm, truncate to strongly cordate at the base, subsessile on a petiole 1–3 mm long, rounded at the apex, dull or slightly lustrous on either side; venation pinnate with the midrib and the main laterals visible on both sides. *Inflorescences* at the nodes, a raceme or spike of (1–)2–5 opposite pairs of flowers; axis 4–14 mm long; pedicels 0–1 mm long; central bract orbicular, 2–2.5 mm long; lateral bracts 2–2.5 mm long, connate, together almost completely enclosing the ovary. *Corolla* in mature bud 6-merous, 70–125(–150) mm long, winged at about four fifths the length, clavate, often angular and truncate at the apex, red or yellow below, often yellow at the neck and red or green above; tube in the open flower 55–110 mm long with the lobes reflexed or twisted 5–10 mm higher. *Anther* 3–8 mm long, obtuse, about equal to the free part of the filament.

Distribution — Thailand; *Malesia*: Peninsular Malaysia, Borneo.

Habitat & Ecology — 0–1000 m altitude; recorded hosts include *Hevea* (commonly), also *Parkia*.

Notes — 1. Closely related to *Macrosolen dianthus* and *M. annamicus* Danser, differing from both in the strongly angular stems and the inflorescences prolonged into a short raceme. In Peninsular Malaysia, where *M. platyphyllus* and *M. dianthus* are sympatric, the differentiation is strongest, *M. platyphyllus* also differing in its strongly cordate subsessile leaves.

2. In the diagnosis of *M. latifolius* Danser cited 3 collections, which are therefore syntypes. *Haviland* 2183 (K) is the most complete specimen, bearing leaves and flowers, and is selected as lectotype of the species name.

18. *Macrosolen pseudoperfoliatus* (Zoll.) Miq.

Macrosolen pseudoperfoliatus (Zoll.) Miq., Fl. Ind. Bat. 1, 1 (1856) 828; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 295; Backer & Bakh. f., Fl. Java 2 (1965) 70. — *Loranthus pseudo-perfoliatus* Zoll., Genees. Nat. Arch. 2 (1845) 578. — *Elytranthe pseudoperfoliata* (Zoll.) Engl., Nat. Pflanzenfam., Nachtr. 1 (1897) 126. — Type: *Zollinger* 2505, Java, 'Goeboegklakah'.

Glabrous. Stem internodes distinctly two-edged when young. *Leaves* opposite; lamina narrowly ovate to ovate, 4–9 by 1–4 cm, usually cordate at the base and sessile, sometimes shortly cuneate at the base to a petiole up to 4 mm long, acuminate and acute at the apex, slightly lustrous above, dull below; venation pinnate with the midrib distinct and the main laterals visible on both sides. *Inflorescences* at the nodes, a sometimes subumbellate raceme of 1–4 opposite pairs of flowers; axis 5–20 mm long; pedicels 1–3 mm long. *Corolla* in mature bud 6-merous, 35–45 mm long, slightly widened upwards, winged above the middle, angular, clavate and acute at the apex, red, sometimes with a dark band at the neck; tube in the open flower 24–30 mm long with the lobes reflexed 4–7 mm higher. *Anther* 2.5–3.5 mm long, acute, about half as long as the free part of the filament. — **Fig. 38c.**

Distribution — *Malesia*: Java.

Habitat & Ecology — 700–2260 m altitude; no hosts recorded.

19. *Macrosolen pusillus* Danser

Macrosolen pusillus Danser, Rec. Trav. Bot. Néerl. 31 (1934) 238. — Type: *Richards* 1993, Sarawak, Dulit Ridge.

Glabrous. *Leaves* opposite; lamina ovate, 4–5.5 by c. 2 cm, almost truncate at the base to a petiole 1–2 mm long, acuminate and acute at the apex, glossy above, dull below; venation pinnate with the midrib distinct above and raised below and the main laterals distinct above and obscure below. *Inflorescences* at the nodes, a raceme of 3 or 4 well-spaced opposite pairs of flowers; axis 10–15 mm long; pedicels 1–2.5 mm long. *Corolla* in mature bud 6-merous, c. 7 mm long, widened upwards, 6-winged, pink; tube in the open flower c. 2.5 mm long with the lobes reflexed c. 2.5 mm higher. *Anther* c. 1 mm long, obtuse, slightly shorter than the free part of the filament.

Distribution — *Malesia*: Borneo (Sarawak). Known from type collection only.

Habitat & Ecology — Open moss forest, 1300 m altitude; no host recorded.

20. *Macrosolen retusus* (Jack) Miq.

Macrosolen retusus (Jack) Miq., Fl. Ind. Bat. I, 1 (1856) 828. — *Loranthus retusus* Jack in Roxb., Fl. Ind., ed. 1, 2 (1824) 212. — Type: *Jack*, Singapore (not located).

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 296].

Glabrous. *Leaves* opposite; lamina narrowly ovate to elliptic or often obovate, 5–10 by 2–7 cm, cuneate at the base to a winged petiole 3–5 mm long, rounded or rarely obtuse at the apex, slightly lustrous above or dull on both sides; venation pinnate with the midrib and the main laterals distinct above and only the midrib dark-coloured and prominent below. *Inflorescences* at the nodes, a raceme of 2–5 opposite pairs of flowers; axis 5–20 mm long; pedicels 1–3 mm long. *Corolla* in mature bud 6-merous, 18–35 mm long, slender and hardly inflated in the lower part, winged at or above the middle, weakly clavate



Fig. 39. *Macrosolen retusus* (Jack) Miq. Borneo, NW Kalimantan, Pasir Pandjang (*Elsener* H 91). Photo A. Elsener, 1965.

and broadly acute at the apex, mostly pink or violet below, green or rarely dark-coloured at the neck and pink to purple above; tube in the open flower 12–24 mm long with the lobes reflexed 2–3 mm higher. *Anther* 1.5–2 mm long, about half as long as the free part of the filament. — **Fig. 39.**

Distribution — *Malesia*: Sumatra, Peninsular Malaysia, Singapore, Borneo.

Habitat & Ecology — Mostly lowlands, 0–250 m altitude, rarely to 1500 m; recorded hosts include *Calophyllum*, *Eugenia*, and *Podocarpus*.

Note — Closely related to *Macrosolen melintangensis*, differing in the duller leaves, mostly rounded at the apex and attenuate into the petiole, and the slightly more robust inflorescence.

21. *Macrosolen robinsonii* (Gamble) Danser

Macrosolen robinsonii (Gamble) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 345. — *Elytranthe robinsonii* Gamble, Kew Bull. 1913 (1913) 45. — Type: *Wray & Robinson 5404*, Malaya, Mt Tahan.

Glabrous. *Leaves* opposite; lamina narrowly ovate to ovate, 5–8(–12) by (1–)2–3.5 (–5) cm, cuneate at the base to a petiole 1–5(–10) mm long, acuminate and acute at the apex, glossy and sometimes red above, dull below; venation pinnate with the midrib and the main laterals distinct above and the midrib prominent and the main laterals visible below. *Inflorescences* at the nodes, an umbellate raceme of 1 or 2 opposite pairs of flowers; axis 1–5 mm long, usually subtended at the base by a few very small acute bracts; pedicels 1–2.5 mm long, bracts c. 1 mm long, the lateral ones partly connate. *Corolla* in mature bud 6-merous, 15–25(–30) mm long, somewhat inflated at the base, cylindric and weakly angular below a distinct neck, clavate and obtuse at the apex, pink or red; tube in the open flower 10–16 mm long with the lobes reflexed or twisted slightly higher. *Anther* 1.5–2 mm long, bluntly acute, about two fifths as long as the free part of the filament.

Distribution — Vietnam; *Malesia*: Peninsular Malaysia.

Habitat & Ecology — 500–1500 m altitude; no hosts recorded.

Note — Similar to *Macrosolen melintangensis*, especially to its Peninsular Malaysian form formerly placed in *M. lowii*, differing in the shorter more subumbellate inflorescence and the inflated corolla tube.

22. *Macrosolen surigaoensis* (Elmer) Danser

Macrosolen surigaoensis (Elmer) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 345. — *Loranthus surigaoensis* Elmer, Leaflet Philipp. Bot. 6 (1913) 1966. — Type: *Elmer 14098* (not located), Mindanao, Mt Urdaneta.

Glabrous. *Leaves* opposite; lamina narrowly ovate, c. 4 cm long, c. 1.25 cm wide, shortly cuneate at the base to a petiole 3–5 mm long, acuminate and acute at the apex, dull on both sides; venation pinnate with the midrib raised and dark coloured below and the main laterals faintly visible on both sides. *Inflorescences* at the nodes, an umbel of 1 pair of flowers; axis c. 10 mm long; pedicels 1–3 mm long. *Corolla* in mature bud 6-merous, c. 12.5 mm long, slightly inflated and weakly 6-ribbed.

Distribution — *Malesia*: Philippines: Mindanao.

Habitat & Ecology — 1875 m altitude; no host recorded.

Note — A doubtful species, known only from the type collection, which is apparently not extant; similar to *Macrosolen cochinchinensis*, apparently differing in smaller leaves and 2-flowered inflorescence.

23. *Macrosolen tetragonus* (Blume) Miq.

Macrosolen tetragonus (Blume) Miq., Fl. Ind. Bat. 1, 1 (1856) 829; Backer & Bakh. f., Fl. Java 2 (1965)

70. — *Loranthus tetragonus* Blume, Bijdr. (1826) 663. — Type: *Blume s.n.*, Java, 'Tjiradjas'.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 300].

Glabrous. Stem internodes quadrangular when young, soon becoming terete. *Leaves* opposite; lamina mostly oblong to suborbicular, mostly 8–12 cm long, mostly 3–6 cm wide, thick, cuneate to truncate at the base and sessile or subsessile or with a petiole to 5 mm long, rounded or rarely attenuate and acute or obtuse at the apex, slightly lustrous above, dull below; venation pinnate with the midrib visible above and prominent below and the main laterals visible on both sides. *Inflorescences* at the nodes, a raceme of (3–) 5–9 opposite pairs of flowers; axis 20–42 mm long; pedicels 1–3 mm long. *Corolla* in mature bud 6-merous, 13–18(–23) mm long, slightly inflated in the lower part, weakly winged near the middle, angular, clavate and obtuse at the apex, yellow or green or becoming red below, green at the neck and green or yellow above; tube in the open flower 6–9(–11) mm long with the lobes reflexed 2–4 mm higher. *Anther* 1.5–2.5 mm long, obtuse, about half as long as the free part of the filament. — **Fig. 38d.**

Distribution — *Malesia*: Sumatra, Java.

Habitat & Ecology — 0–1600 m altitude; no hosts recorded.

Note — Similar to *Macrosolen cochinchinensis*, differing in the angular young stems, thicker leaves and more robust inflorescences.

24. *Macrosolen* × *tubiflorus* (Ridl.) Danser

Macrosolen × *tubiflorus* (Ridl.) Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 303. — *Elytranthe tubiflora* Ridl., J. Roy. As. Soc., Str. Br. 86 (1922) 306 ('*tubaeiflora*'). — Type: *Yapp 501*, Perak, Mt Inas.

Macrosolen splendidus Danser, Rec. Trav. Bot. Néerl. 31 (1934) 234. — Type: *Clemens 28530*, Sabah, Mt Kinabalu.

Glabrous. *Leaves* opposite; lamina ovate, 10–20 by 4–8 cm, cuneate to truncate at the base to a petiole 4–10 mm long, mostly acuminate and acute at the apex, lustrous or glossy above, dull below; venation pinnate with the midrib distinct and the main laterals visible on both sides. *Inflorescences* at the nodes, a raceme of 2–7 opposite pairs of flowers; axis 10–20 mm long, subtended at the base by an involucre of short broadly triangular bracts; pedicels appressed to the axis, 1–4 mm long, bracts keeled, acute, 2–3 mm long. *Corolla* in mature bud 6-merous, 70–90 mm long, gradually widened upwards to a neck, weakly clavate and angular above, broadly acute at the apex, mostly

red below and usually longitudinally striped paler and darker above; tube in the open flower 50–65 mm long with the lobes reflexed 8–12 mm higher. *Anther* 5–6 mm long, slightly sagittate at the base, acute, about half as long as the free part of the filament. — **Fig. 37a, b.**

Distribution — *Malesia*: Peninsular Malaysia, Borneo.

Habitat & Ecology — Mostly in highlands from 1000 to 2100 m altitude but occasionally down to 180 m; the only recorded host is *Eugenia*.

Note — The species shows features of both *Macrosolen acunae* (especially in the inflorescence and flowers) and *M. formosus* (especially in the leaves); it is possibly of hybrid origin, although now perhaps persisting as a stable recognizable form, and has been designated accordingly. The species can be distinguished from *M. formosus* by its shorter inflorescence with more flowers on crowded and more appressed pedicels, and its narrower more acute corolla with weaker wings and ridges.

PAPUANTHES

Papuanthes Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 360. — Type species: *Papuanthes albertisii* (Tiegh.) Danser.

[For synonymy see Barlow, Austral. J. Bot. 22 (1974) 598].

Aerial stem-parasitic shrubs, robust, with epicortical runners bearing secondary haustoria. *Leaves* opposite. *Inflorescence* capitate, consisting of several flowers in two rows at the apex of a common peduncle, enclosed by two foliaceous bracts which are connate at the margins over them during development; flowers each on an articulate pedicel with a small bract at the apex of the distal segment and sometimes also at the apex of the proximal segment. *Corolla* 6-merous, gamopetalous, almost regular. *Anthers* basifixed, immobile. *Style* simple, with a knob-like stigma. *Fruit* ovoid. — **Fig. 40.**

Distribution — One species endemic to New Guinea.

Habitat & Ecology — Humid forests, from lowlands to 1550 m altitude; host specificity is probably low.

Morphology — The normally developed pairs of leaves sometimes alternate with scale leaves at intervening nodes just above the leaf-bearing nodes, so that the leaves may appear superposed (see note under *Macrosolen*).

The individual flowers, on articulate pedicels, may be homologous with the reduced inflorescences of *Sogerianthe* (see there). If so, the capitate involucrate conflorescence is a complex secondarily compound structure which probably represents a modified shoot system.

Taxonomy & Phylogeny — Like *Sogerianthe*, *Papuanthes* has $x = 9$ and relatively large chromosomes. It is probably a specialized local derivative of the Papuasian stock of which *Amyema* is the core. The most closely related genus is probably *Sogerianthe*, with which it shares gamopetalous corollas and articulate pedicels, and from which it differs in its compound capitate inflorescence.

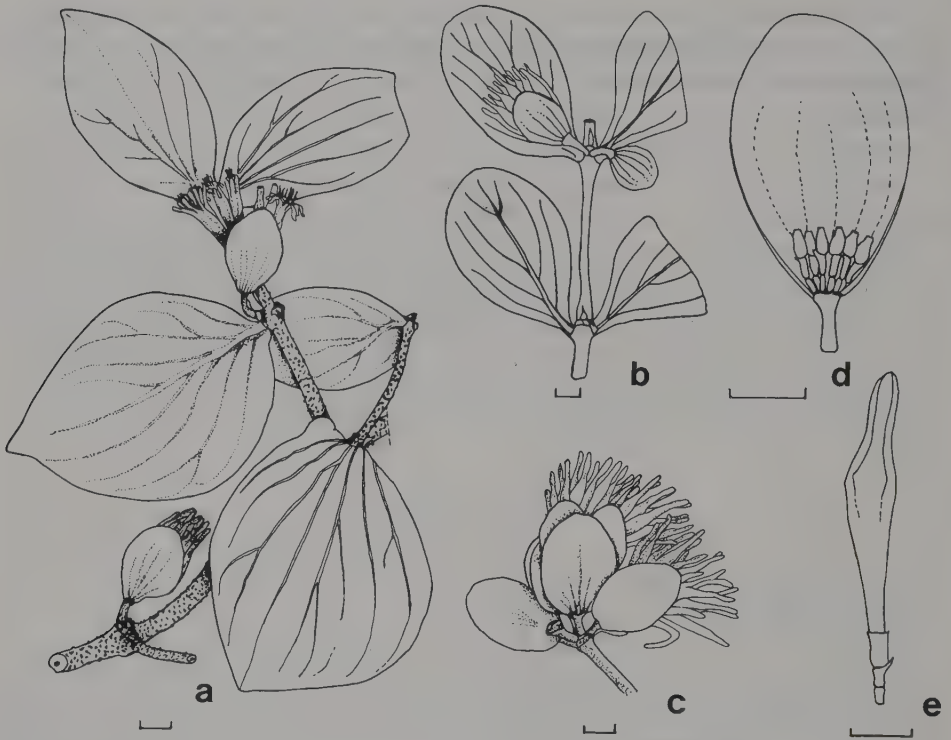


Fig. 40. *Papuanthes albertisii* (Tiegh.) Danser. a–c. Portions of stems with inflorescences; d. inflorescence with young fruits, sectional view; e. flower bud (Collections not cited). a, c Redrawn from Barlow (1981), b, d, e redrawn from Barlow (1974). Scale bars represent 1 cm.

***Papuanthes albertisii* (Tiegh.) Danser**

Papuanthes albertisii (Tiegh.) Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 360; Barlow, Austral. J. Bot. 22 (1974) 605; in Handb. Fl. Papua New Guinea 2 (1981) 249. — *Diplatia albertisii* Tiegh., Bull. Soc. Bot. France 41 (1894) 539. — Type: *d'Albertis s. n.*, Papua New Guinea, Fly River. [For additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 605].

Glabrous. *Leaves* opposite, often seemingly superposed through extreme contraction of every second internode and reduction of every second pair of leaves to scales; lamina ovate, 8–20 by 5–12 cm, thick, truncate to slightly cordate at the base, sessile or with a terete petiole to 4 mm long, obtuse at the apex, dull on both sides; venation pinnate with the midrib and main laterals visible on both sides. *Inflorescences* at the nodes, a head of (8–)10–12(–15) flowers; peduncle stout, 4–12 mm long, 3–4 mm thick, flattened at the apex; involucre bracts ovate to orbicular, 25–40 by 20–25 mm, obtuse or rounded; pedicels 1.5–2 mm long, much enlarged under the fruit, articulate above the middle, with acute bracts c. 1.5 mm long. *Corolla* in mature bud 40–65 mm long, widened upwards, narrowed near the apex, rounded, pink or red; tube in the open flower 25–40

mm long with the petals reflexed 3–5 mm higher. *Anther* 3–4 mm long, about equal to the free part of the filament. — **Fig. 40.**

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Humid forests and gallery forests, from 0 to 1550 m altitude; recorded hosts include *Ficus*, *Myristica*, and *Terminalia*.

SCURRULA

Scurrula L., Sp. Pl. (1753) 110. — Type species: *Scurrula parasitica* L.
[For synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 427; Philipp. J. Sc. 58 (1935) 116].

Aerial stem-parasitic shrubs, more or less clothed in a tomentum of stellate and dendritic hairs, slender to moderately robust, with epicortical runners bearing secondary haustoria. *Leaves* opposite, different above and below (especially with respect to indumentum). *Inflorescence* a simple 3- to 10-flowered raceme of decussate flowers, rarely 2-flowered and apparently umbellate; bract single under each flower, simple. *Corolla* 4-merous, gamopetalous, zygomorphic, with the tube curved prior to anthesis, deeply split on the inner side of the curve; lobes reflexed to the outer side at anthesis. *Anthers* basifixed, immobile. *Style* simple, with a knob-like stigma. *Fruit* obovoid, club-like, distinctly stipitate. — **Fig. 41.**

Distribution — About 20 species from India to Taiwan and Malesia. In *Malesia* 8 species, with a centre of richness and diversity in Java (7 species).

Habitat — Humid and open forests and disturbed sites, from lowlands to 3000 m. Some species occur predominantly or exclusively in highlands above 1000 m.

Ecology — In Malesia some species are aggressive, apparently with broad host ranges including cultivated trees. The hosts also include other *Loranthaceae*; such epiparasitism is also common in other genera such as *Amyema* and *Lysiana* (*Loranthaceae*) and *Viscum* and *Notothixos* (*Viscaceae*), and probably results from a sharing of the bird dispersal agents.

Taxonomy & Phylogeny — The genus is related to *Dendrophthoe*, differing in fruit structure and the small more strongly zygomorphic 4-merous flowers. For discussion of Afro-Asian origins, see Barlow (1990).

The genus is also closely related to, and difficult to delineate from, the sympatric genus *Taxillus* (see Barlow 1990). Ban, Tap Chi Sinh HOC 16, 4 (1994) 49, 54, has without discussion apparently proposed union of *Scurrula* and *Taxillus*, but he erroneously placed *Scurrula* (1753) in synonymy under *Taxillus* (1895).

KEY TO THE SPECIES

- 1a. Corolla less than 20 mm long 2
- b. Corolla more than 20 mm long 5
- 2a. Indumentum of the corolla dense, with a layer of longer dendritic hairs above the shorter ones. 3

- b. Indumentum of the corolla sparse to dense, lacking a layer of longer dendritic hairs above the shorter ones 4
- 3a. Corolla in the mature bud robust, obtuse, mostly 8–14 mm long **4. *S. ferruginea***
- b. Corolla in the mature bud slender to moderately robust, clavate, acute, mostly 12–24 mm long **6. *S. x montana***
- 4a. Indumentum generally pale-coloured, predominantly cream, less often a greyish or dark ochre; leaf lamina 5–10 cm long; corolla mostly 13–20 mm long **2. *S. atropurpurea***
- b. Indumentum very variable in colour from cream to dark reddish brown but predominantly of darker hues; leaf lamina 3–7 cm long; corolla mostly 8–16 mm long ... **8. *S. parasitica***
- 5a. Bract ovate or obovate, concave, longer than and enclosing the ovary **7. *S. oortiana***
- b. Bract linear to narrowly ovate or deltoid, flat or concave, mostly shorter than and not enclosing the ovary 6
- 6a. Leaf lamina less than 3 cm long; inflorescence of 2 equal-aged flowers, resembling a simple umbel **3. *S. didyma***
- b. Leaf lamina more than 3 cm long; inflorescence of 2 or more unequal-aged flowers, racemose 7
- 7a. Corolla in the mature bud robust, not or only weakly clavate towards the apex, 8–14 (–23) mm long **4. *S. ferruginea***
- b. Corolla in the mature bud slender, gradually and distinctly clavate towards the apex, 19–45 mm long 8
- 8a. Inflorescence a subumbellate raceme, with a short axis bearing 2 or 3 nearly equal-aged flowers near the apex; corolla obtuse; leaf lamina folded; indumentum creamy white **1. *S. aphodastrica***
- b. Inflorescence distinctly racemose, with an axis usually 12–20 mm long bearing more than 3 flowers developing successively; corolla acute; leaf lamina flat; indumentum ochre to reddish brown 9
- 9a. Corolla up to 24 mm long, its indumentum with a layer of longer dendritic hairs above the shorter ones **6. *S. x montana***
- b. Corolla mostly more than 24 mm long, its indumentum lacking a layer of longer dendritic hairs above the shorter ones **5. *S. lepidota***

1. *Scurrula aphodastrica* Barlow

Scurrula aphodastrica Barlow, Blumea 36 (1991) 68. — Type: *Schmutz* 2895, Flores.

Young parts with a dense creamy white indumentum of short stellate and dendritic hairs, becoming sparse on adult stems, leaves and corollas. *Leaves* opposite; lamina narrowly elliptic, 4–6 by 1.5–2.4 cm, attenuate at the base to an obscure winged petiole

3–4 mm long, often infolded along the midrib, obtuse or shortly rounded at the apex; venation obscure except for the midrib and a few major laterals visible on both sides. *Inflorescences* several at the nodes, arising successively from gall-like swellings, a 2- or 3-flowered subumbellate raceme; axis 1–2(–5) mm long; pedicels 2–4 mm long; bract deltoid, erect, c. 1 mm long. *Corolla* in mature bud 22–30 mm long, slender, narrowly clavate and obtuse at the apex; tube 16–24 mm long, split to the middle or lower. *Anther* 0.7–1 mm long, recurved, about half as long as the free part of the filament. *Fruit* 12–15 mm long including a stipe 6–10 mm long, truncate at the apex.

Distribution — *Malesia*: Lesser Sunda Islands (Flores).

Habitat & Ecology — 50–500 m altitude; recorded hosts include *Bridelia* and *Helicteres*.

Note — Closely related to *Scurrula atropurpurea*, differing in narrower folded leaves, subumbellate few-flowered inflorescences in dense clusters, and longer flowers.

2. *Scurrula atropurpurea* (Blume) Danser

Scurrula atropurpurea (Blume) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 349; 11 (1931) 429; Backer & Bakh. f., Fl. Java 2 (1965) 74; Barlow, Blumea 36 (1991) 70. — *Loranthus atropurpureus* Blume, Verh. Bat. Genootsch. 9 (1823) 186. — *Taxillus atropurpureus* (Blume) Ban, Tap Chi Sinh HOC 16, 4 (1994) 49. — Type: *Blume s.n.*, Java.

Loranthus philippinensis Cham. & Schltdl., Linnaea 3 (1828) 204. — *Scurrula philippinensis* (Cham. & Schltdl.) G. Don, Gen. Hist. 3 (1834) 422; Danser, Philipp. J. Sc. 58 (1935) 121; Backer & Bakh. f., Fl. Java 2 (1965) 74. — *Taxillus philippinensis* (Cham. & Schltdl.) Ban, Tap Chi Sinh HOC 16, 4 (1994) 50. — Type: *Chamisso s.n.*, Philippines.

[For extensive additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 429; Philipp. J. Sc. 58 (1935) 121; excluding *Loranthus* (*Dendrophthoe*, *Scurrula*) *junghuhnii* = *Scurrula lepidota*; excluding *Loranthus* (*Dendrophthoe*, *Cichlanthus*) *repandus* = *Scurrula parasitica*.]

Young parts with a dense cream or rarely greyish to dark ochre indumentum of stellate hairs, becoming sparse on adult stems, leaf upper surfaces and flowers. *Leaves* opposite; lamina elliptic to obovate, 5–10 by 2.3–5 cm, cuneate to slightly cordate at the base to a petiole 6–12 mm long, usually rounded at the apex; venation obscure except for the midrib and a few major laterals visible above. *Inflorescences* several at the nodes, a (2–)4–6(–8)-flowered raceme; axis 5–12 mm long; pedicels 2–3 mm long; bract deltoid, erect, c. 1.5 mm long. *Corolla* in mature bud (11–)13–20(–24) mm long, slender, narrowly clavate and acute at the apex; tube 7–15 mm long, deeply split. *Anther* c. 1 mm long, about half as long as the free part of the filament. *Fruit* 8–9 mm long including a thick stipe 2–3 mm long, contracted at the apex. — **Fig. 41.**

Distribution — Thailand to Vietnam; *Malesia*: Java, Philippines, Lesser Sunda Islands (Bali, Sumbawa), Moluccas.

Habitat & Ecology — Mostly 0–600 m altitude, less frequently to 2300 m; recorded hosts include *Acacia*, *Averrhoa*, *Grewia*, *Myristica*, and *Terminalia*.

Note — Conspecific with *Scurrula philippinensis*; for discussion of species circumscription see Barlow, Blumea 36 (1991) 71.

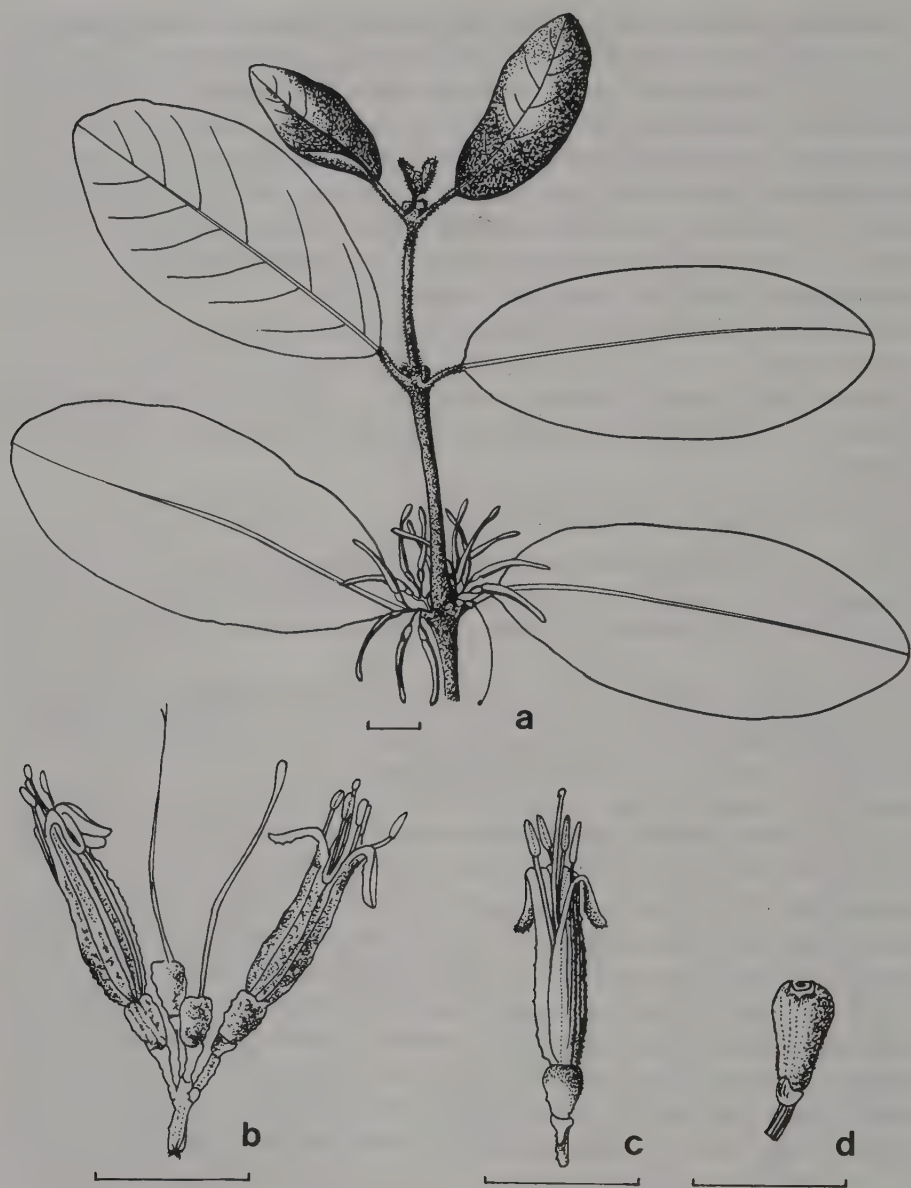


Fig. 41. *Scurrula atropurpurea* (Blume) Danser. a. Flower-bearing twig; b. inflorescence; c. flower; d. fruit (Collections not cited). a Redrawn from Blume (1830), b–d redrawn from Danser (1931). Scale bars represent 1 cm.

3. *Scurrula didyma* Barlow

Scurrula didyma Barlow, Blumea 36 (1991) 72. — Type: ten Houten & Coert 40.28 (Herb. Coert 1570), Java, 'Batjangvlakte'.

Young parts with a short dense dark red-brown indumentum of stellate hairs, soon glabrescent on adult stems and leaf upper surfaces. *Leaves* opposite; lamina elliptic to ovate, 2–2.5 by 1–1.5 cm, cuneate at the base to a petiole c. 5 mm long, rounded at the apex; venation obscure except for the midrib raised in the lower part on the underside. *Inflorescences* produced successively at the nodes, a 2-flowered umbel; axis 1–3 mm long; pedicels 4–7 mm long; bract narrow, concave, erect, rounded, c. 1.5 mm long. *Corolla* in mature bud c. 25 mm long, robust, slightly inflated above the base, obtuse at the apex; open flower not seen. *Fruit* c. 10 mm long including a stipe c. 5 mm long, contracted at the apex.

Distribution — *Malesia*: Java.

Habitat & Ecology — Highlands from 2500 to 2950 m altitude; the only recorded host is *Vaccinium*.

Note — Possibly related to *Scurrula ferruginea*, but very distinct in its 2-flowered inflorescence with equal-aged flowers.

4. *Scurrula ferruginea* (Jack) Danser

Scurrula ferruginea (Roxb. ex Jack) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 350; 11 (1931) 432; Backer & Bakh. f., Fl. Java 2 (1965) 74; Barlow, Blumea 36 (1991) 73. — *Loranthus ferrugineus* Roxb. ex Jack, Mal. Misc. 1 (1820) 279. — *Taxillus ferrugineus* (Jack) Ban, Tap Chi Sinh HOC 16, 4 (1994) 49. — Type: Jack, Sumatra (probably not extant).

[For further synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 432; Philipp. J. Sc. 58 (1935) 123].

Young parts with a dense ochre to reddish brown indumentum of short stellate and longer dendritic hairs, becoming sparse on adult stems and leaf upper surfaces. *Leaves* opposite; lamina elliptic to ovate or slightly obovate, (3–)5–10 by (1.5–)2–5.5 cm, cuneate to weakly cordate at the base to a petiole 2–6(–10) mm long, obtuse or rounded at the apex; venation obscure except for the midrib and a few major laterals visible above. *Inflorescences* several at the nodes, a 2- to 5-flowered raceme; axis 2–10(–15) mm long; pedicels 0.5–2.5(–4) mm long; bract narrow, erect, 1–2(–3) mm long. *Corolla* in mature bud (6–)8–14(–23) mm long, straight or slightly curved, usually robust, rarely relatively slender and weakly clavate, obtuse to truncate at the apex; tube 5–15 mm long, split to the middle or lower. *Anther* 0.5–1 mm long, about half as long as the free part of the filament. *Fruit* 8–10 mm long including a stipe 4–6 mm long, rounded at the apex.

Distribution — India to southern China and Vietnam; *Malesia*: Western parts, extending eastwards as far as Palawan, Celebes and Flores.

Habitat & Ecology — Primary forests and disturbed sites, mostly 0–1000 m altitude, less frequently to 1850 m; recorded hosts include *Coffea*, *Melastoma*, *Pithecellobium*, and *Saurauia*.

Note — Probably hybridizes with other *Scurrula* species; for discussion see Barlow, Blumea 36 (1991) 73.

5. *Scurrula lepidota* (Blume) G. Don

- Scurrula lepidota* (Blume) G. Don, Gen. Hist. 3 (1834) 422; Backer & Bakh. f., Fl. Java 2 (1965) 73. — *Loranthus lepidotus* Blume, Verh. Bat. Genootsch. 9 (1823) 191. — Type: *Blume s.n.*, Java.
- Loranthus obovatus* Blume, Bijdr. (1826) 663. — *Scurrula obovata* (Blume) G. Don, Gen. Hist. 3 (1834) 422; Backer & Bakh. f., Fl. Java 2 (1965) 74. — Type: *Reinwardt 1308*, Timor.
- Loranthus kalahiensis* Korth., Verh. Bat. Genootsch. 17 (1839) 271. — *Scurrula kalahiensis* (Korth.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 351. — Type: *Korthals s.n.*, Borneo, Mt Kalahien.
- Loranthus ellipticus* Korth., Verh. Bat. Genootsch. 17 (1839) 272. — Type: *Korthals s.n.*, Borneo, Mt Kramat.
- Loranthus medinensis* Molk. in Miq., Pl. Jungh. (1852) 112. — *Scurrula medinensis* (Molk.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 352. — Type: *Junghuhn s.n.*, Java, Mt Ungarang.
- Loranthus junghuhnii* Molk. in Miq., Pl. Jungh. (1852) 113. — *Dendrophthoe junghuhnii* (Molk.) Miq., Fl. Ind. Bat. 1, 1 (1856) 817. — *Scurrula junghuhnii* (Molk.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 351. — Type: *Junghuhn s.n.*, Java, Mt Ungarang.
- [For further synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 437, 439–442; Barlow, Blumea 36 (1991) 75].

Young parts with a dense ochre to reddish brown indumentum of short stellate hairs, rarely with some longer dendritic ones soon disappearing, becoming sparse on adult stems, leaves and corollas. *Leaves* opposite; lamina narrowly elliptic to ovate or obovate, (3.5–)6–12 by (1.8–)3–5.5 cm, shortly cuneate to weakly cordate at the base to a petiole (3–)6–10(–15) mm long, obtuse or rounded at the apex; venation obscure except for the midrib and a few major laterals visible on both sides. *Inflorescences* several at the nodes, a (2–)4–8-flowered raceme; axis (2–)12–20(–25) mm long; pedicels (1–)4–7 mm long; bract elliptic, erect, variable, (0.5–)1–1.5(–3) mm long. *Corolla* in mature bud 19–45 mm long, usually slender, clavate, angular and acute at the apex; tube 13–30 mm long, sometimes slightly inflated, split to the middle or lower. *Anther* 1–2(–4) mm long, usually about two thirds as long as the free part of the filament. *Fruit* 8–12 mm long including a stipe 5–7 mm long, rounded at the apex.

Distribution — *Malesia*: Sumatra, Borneo, Java, Lesser Sunda Islands eastwards to Timor.

Habitat & Ecology — Mostly in highlands 1000–2400 m altitude, less frequently down to sea level, especially in Borneo; recorded hosts include *Ficus*, *Photinia*, and *Viburnum*.

Note — For discussion on species circumscription and conspecificity with *Scurrula junghuhnii*, *S. kalahiensis*, *S. medinensis* and *S. obovata* see Barlow, Blumea 36 (1991) 75.

6. *Scurrula x montana* Danser

- Scurrula x montana* Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 441; Backer & Bakh. f., Fl. Java 2 (1965) 74; Barlow, Blumea 36 (1991) 77. — Type: *Koorders 43003b*, lecto, Java, Gendingwaloh.

Young parts with a dense reddish brown indumentum of short stellate and dendritic hairs, becoming sparse on adult stems and leaf upper surfaces. *Leaves* opposite; lamina variable, mostly elliptic to ovate, 2.5–12 by 1.5–7 cm, truncate to weakly cordate at the base, sessile or with a petiole to 15 mm long, often undulate at the margin, rounded at

the apex; venation obscure except for the midrib and a few major laterals visible above. *Inflorescences* few at the nodes, a 2- to 12-flowered raceme; axis variable, 3–22 mm long, usually robust; pedicels 2–3 mm long; bracts very variable, usually narrowly deltoid or ovate, sometimes foliaceous, flat or concave, acute to rounded, shorter or longer than the ovary. *Corolla* in mature bud 12–24 mm long, relatively slender, clavate and acute or obtuse at the apex; tube 7–16 mm long, split to the middle or lower. *Anther* 1–2 mm long, about equal to the free part of the filament. *Fruit* 9–10 mm long including a stipe 5–6 mm long, contracted at the apex.

Distribution — *Malesia*: Sumatra, Java.

Habitat & Ecology — Highlands from 1275 to 2500 m altitude; probably commonly parasitic on *Casuarina*.

Note — Closely related to *Scurrula lepidota* and *S. oortiana*, and probably of hybrid origin; for discussion see Barlow, *Blumea* 36 (1991) 78.

7. *Scurrula oortiana* (Korth.) Danser

Scurrula oortiana (Korth.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 352; 11 (1931) 443; Backer & Bakh.f., Fl. Java 2 (1965) 73; Barlow, *Blumea* 36 (1991) 79. — *Loranthus oortianus* Korth., Verh. Bat. Genootsch. 17 (1839) 269. — *Dendrophthoe oortiana* (Korth.) Miq., Fl. Ind. Bat. 1, 1 (1856) 813. — Type: *Korthals s.n.*, lecto, Sumatra, Mt Singgalang.

Loranthus korthalsii Molck. in Miq., Pl. Jungh. (1852) 110. — *Dendrophthoe korthalsii* (Molck.) Miq., Fl. Ind. Bat. 1, 1 (1856) 814. — *Scurrula korthalsii* (Molck.) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 351; 11 (1931) 439; Backer & Bakh.f., Fl. Java 2 (1965) 73. — Type: *Junghuhn s.n.*, Java.

Young parts with a dense golden or red-brown indumentum of short stellate and dendritic hairs, becoming sparse on adult stems and leaves. *Leaves* opposite; lamina oblong to ovate or rarely obovate, mostly 9–14 cm long, 4.5–6 cm wide, truncate or weakly cordate at the base to a petiole 3–8 mm long, often undulate at the margin, obtuse or rounded at the apex; venation obscure except for the midrib and a few major laterals visible on both sides. *Inflorescences* few at the nodes, a 4- to 12-flowered raceme; axis 8–30(–40) mm long; pedicels 3–9 mm long; bract elliptic to nearly orbicular, concave, rounded, 5–7 mm long, enclosing the ovary. *Corolla* in mature bud 15–35(–43) mm long, slender, clavate and acute or obtuse at the apex; tube 10–25(–29) mm long, split to the middle or lower. *Anther* 2–3 mm long, about equal to the free part of the filament. *Fruit* 11–14 mm long including a stipe 7–10 mm long, truncate at the apex.

Distribution — *Malesia*: Sumatra, Java.

Habitat & Ecology — Highlands from 1000 to 2050 m altitude; recorded hosts include *Citrus*, *Eugenia*, *Ficus*, and *Saurauia*.

Note — For discussion on species circumscription and conspecificity of *Scurrula korthalsii*, see Barlow, *Blumea* 36 (1991) 80.

8. *Scurrula parasitica* L.

Scurrula parasitica L., Sp. Pl. (1753) 110; Danser, Philipp. J. Sc. 58 (1935) 118; Backer & Bakh.f., Fl. Java 2 (1965) 74; Barlow, *Blumea* 36 (1991) 80. — *Taxillus parasiticus* (L.) Ban, Tap Chi Sinh HOC 16,4 (1994) 50. — Type: in LINN.

Loranthus fuscus Blume, Verh. Bat. Genootsch. 9 (1823) 192. — *Scurrula fusca* (Blume) G. Don, Gen. Hist. 3 (1834) 420; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 434. — Type: *Blume s.n.*, Java.

Loranthus repandus DC., Prodr. 4 (1830) 300. — *Dendrophthoe repanda* (DC.) G. Don, Gen. Hist. 3 (1834) 420. — *Cichlanthus repandus* (DC.) Tiegh., Bull. Soc. Bot. France 42 (1895) 253. — Type: *Blume s.n.*, Java.

[For extensive further synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 434; 16 (1938) 34; Philipp. J. Sc. 58 (1935) 118].

Young parts with a sparse to dense grey to dark brown or rarely paler indumentum of short stellate hairs, soon becoming sparse on adult stems and leaves. *Leaves* opposite; lamina narrowly ovate to obovate, 3–7(–9) by 1.5–3.5(–4.5) cm, thin, cuneate to truncate at the base to a petiole 3–10 mm long, acute, obtuse or rounded at the apex; venation obscure except for the midrib and a few major laterals visible on both sides. *Inflorescences* several at the nodes, a 2- to 6-flowered raceme; axis 1–6 mm long; pedicels 1–5 mm long; bract narrow, erect, 1–3 mm long. *Corolla* in mature bud 8–16 mm long, slender, weakly clavate and acute at the apex; tube 6–12 mm long, split to the middle or lower. *Anther* 0.7–1.5 mm long, about two thirds as long as the free part of the filament. *Fruit* 8–10 mm long including a stipe 4–8 mm long, rounded at the apex.

Distribution — India eastwards to China and Vietnam; *Malesia*: western parts, extending eastwards as far as the Philippines, Moluccas and Timor.

Habitat & Ecology — Common in a range of primary forests and disturbed sites, mostly from 0 to 1800 m altitude, less frequently to 2250 m; recorded hosts include *Annona*, *Dalbergia*, *Dendrophthoe*, *Glochidion*, *Manglietia*, *Melastoma*, *Moringa*, *Nerium*, *Schima*, and *Xylocarpus*.

Note — Probably hybridizes with other *Scurrula* species; for discussion see Barlow, *Blumea* 36 (1991) 81.

SOGERIANTHE

Sogerianthe Danser, Verh. Akad. Wet. Amst. Afd. Natuurk. 29 (1933) 106; Bull. Jard. Bot. Buitenzorg III, 14 (1936) 95. — Type species: *Sogerianthe sogerensis* (S. Moore) Danser. [For synonymy see Barlow, *Austral. J. Bot.* 22 (1974) 599].

Aerial stem-parasitic shrubs, with epicortical runners bearing secondary haustoria. *Leaves* opposite; venation pinnate but somewhat curvinerved. *Inflorescence* a solitary flower on an articulate pedicel (sometimes apparently not articulate owing to reduction of the peduncular segment); bracts 2 or 3 under the flower, free or connate. *Corolla* 6-merous, gamopetalous, regular. *Anthers* basifixed, immobile. *Style* simple, with a knob-like stigma. *Fruit* ovoid. — **Fig. 42.**

Distribution — Five species in New Guinea and Solomon Islands. In *Malesia* 4 species, all occurring in eastern mainland New Guinea, some extending to the Bismarck Archipelago.

Habitat & Ecology — Mostly in humid forests, from 0 to 2230 m altitude but more common in lowlands.

Taxonomy & Phylogeny — *Sogerialthe* has $x = 9$ and relatively large chromosomes; it is probably a specialized local derivative of the Papuan stock of which *Amyema* is the core. It differs from *Amyema* in its strongly gamopetalous corolla. The distinctive articulate floral pedicels also occur as an extreme inflorescence reduction in *Amyema*, notably in New Guinean species such as *A. finisterrae* and *A. hastifolia*. For discussion see Barlow, Austral. J. Bot. 14 (1966) 453.

KEY TO THE SPECIES

- 1a. Bracts united into a shallow 3-lobed cup; pedicel mostly not visibly articulate **1. *S. cupuliformis***
- b. Bracts free or with two of them partly or completely fused and placed opposite to and slightly to strongly imbricate with the third; pedicel obsolete or up to 7 mm long, when visible usually articulate near or above the middle 2
- 2a. Bracts 1–1.5 mm long, not completely enclosing the ovary; pedicel mostly 4–7 mm long, articulate above the middle, rarely obsolete **4. *S. sogerensis***
- b. Bracts 2–4 mm long, imbricate, enclosing the ovary; pedicel 0.5–2 mm long, articulate near the middle or with the lower segment obsolete and thus apparently not articulate 3
- 3a. Leaves long acuminate, brown tomentose below; corolla in bud ferrugineous, finely acute **2. *S. ferruginea***
- b. Leaves obtuse to acute and shortly acuminate, more or less glabrous below; corolla in bud glabrous, rounded, clavate **3. *S. sessiliflora***

1. *Sogerialthe cupuliformis* Barlow

Sogerialthe cupuliformis Barlow, Austral. J. Bot. 22 (1974) 601; in Handb. Fl. Papua New Guinea 2 (1981) 251. — Type: *Brass* 25487, Normanby I.

Glabrous except for the inflorescence and ovary shortly brown tomentose. *Leaves* opposite; lamina ovate, 6–15 by (2–)4–7 cm, cuneate at the base, sessile or with a short obscure petiole, acuminate and acute at the apex, dull on both sides; venation distinct on both sides. *Inflorescences* several to many at the nodes; pedicel (1–)2–3(–4) mm long, not articulate; bracts 3, 1–1.5 mm long, connate at the margins to a shallow 3-lobed cup. *Corolla* in mature bud 24–32 mm long, inflated towards the middle, weakly clavate and acute at the apex, very pale yellow or green below and orange to red above; tube in the open flower 14–18 mm long with the petals reflexed 5–8 mm higher. *Anther* 2–4 mm long, shorter than or equal to the free part of the filament.

Distribution — New Britain, New Ireland, Bougainville, D’Entrecasteaux Islands, Louisiade Archipelago.

Habitat & Ecology — 0–900 m altitude; the only recorded host is *Ficus*.

Note — Closely related to *Sogerialthe sogerensis*, with which it has a geographical replacement pattern, differing in the more nearly sessile leaves, non-articulate pedicel and more regular bracteal cup.

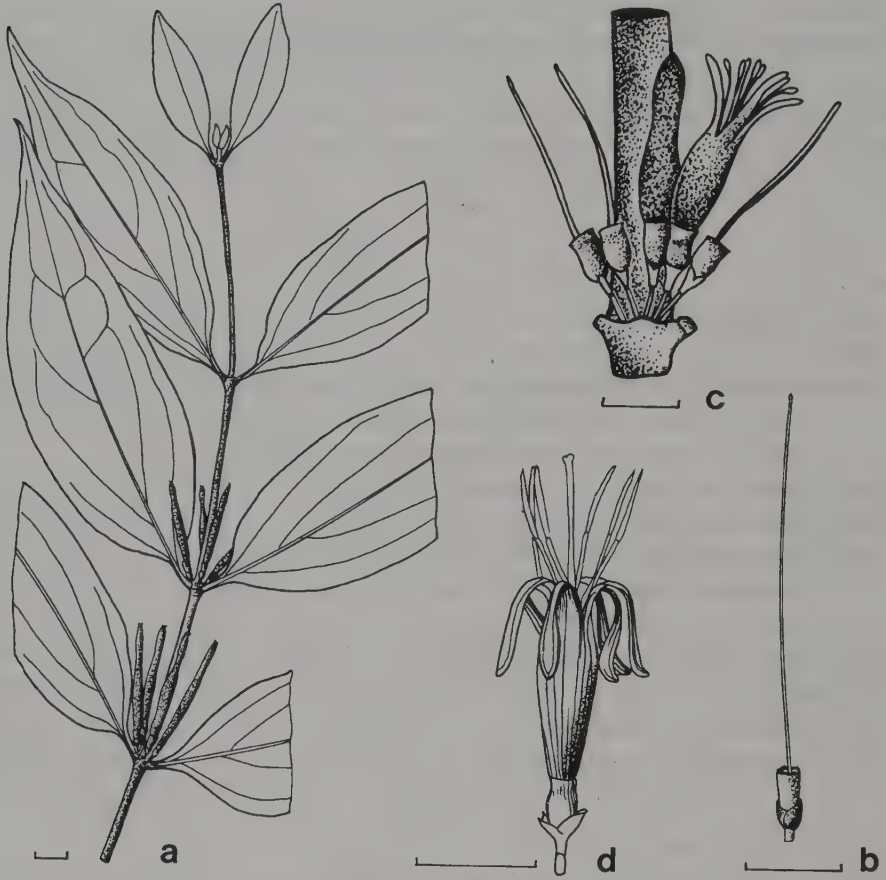


Fig. 42. *Sogerianthe ferruginea* Danser. a. Twig with inflorescences; b. inflorescence with corolla and stamens fallen. — *S. sogerensis* (S. Moore) Danser. c. Part of stem with inflorescences; d. inflorescence with open flower (a, b: Carr 13917; c: not cited, d: Forbes 715). a, b Redrawn from Danser (1938), c redrawn from Barlow (1974), d redrawn from Danser (1931). Scale bars represent 1 cm.

2. *Sogerianthe ferruginea* Danser

Sogerianthe ferruginea Danser, Blumea 3 (1938) 49. — Type: Clemens 4646, Papua New Guinea, Ogeramang to Malang.

Young parts, inflorescences and flowers with a dense rusty tomentum, the stems and leaf upper surfaces eventually glabrescent. *Leaves* opposite; lamina ovate, 9–16 by 4–7 cm, attenuate or cuneate at the base to a petiole 4–10 mm long, acuminate and acute at the apex, dull and dark green above, paler below under the rusty indumentum; midrib and main laterals distinct above. *Inflorescences* several at the nodes; pedicel 0.5–2 mm long, articulate near the middle or with the peduncular segment obsolete and then apparently not articulate; bracts apparently 2 (owing to complete or nearly complete fusion of

two of the three bracts), 2–3 mm long, 2–4 mm wide, acute, imbricate and enveloping the ovary. *Corolla* in mature bud 28–38 mm long, slightly inflated towards the middle, weakly clavate and acute at the apex, pink or red, sometimes yellow above; tube in the open flower 16–22 mm long with the petals reflexed 5–8 mm higher. *Anther* c. 3 mm long, shorter than the free part of the filament. — **Fig. 42a, b.**

Distribution — *Malesia*: New Guinea (mainland).

Habitat & Ecology — Mesic forests from 900 to 1375 m altitude; no hosts recorded.

Notes — Treated by Barlow (1974) as conspecific with *Sogerianthe sessiliflora*, but examination of additional material of the latter confirms the differences recognized by Danser. Closely related to *S. sessiliflora*, differing in longer, acuminate leaves brown tomentose on the underside, and ferrugineous corolla finely acute in bud.

3. *Sogerianthe sessiliflora* (Danser) Danser

Sogerianthe sessiliflora (Danser) Danser, Verh. Akad. Wet. Amst. Afd. Natuurk. 29 (1933) 106; Barlow, Austral. J. Bot. 22 (1974) 602; in Handb. Fl. Papua New Guinea 2 (1981) 251. — *Amyema sessiliflora* Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 346. — Type: *Brass* 1377, lecto, New Guinea, Karaudi.

[For additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 602, excluding *S. ferruginea*].

Glabrous or the flower buds rusty tomentose. *Leaves* opposite; lamina ovate, 6–14 by 3–5 cm, cuneate to truncate at the base to a petiole 3–5 mm long, shortly acuminate and acute or obtuse at the apex, dull on both sides; venation distinct, slightly more prominent below. *Inflorescences* many at the nodes; pedicel 0.5–2 mm long, articulate near the middle or with the peduncular segment obsolete and then apparently not articulate; bracts apparently 2 (owing to complete or nearly complete fusion of two of the three bracts), 2–3 mm long, 2–4 mm wide, acute, imbricate and enveloping the ovary. *Corolla* in mature bud 25–35 mm long, inflated below the middle, narrowed to a neck, weakly clavate and rounded at the apex, cream or very pale pink below and orange or red above; tube in the open flower 11–15 mm long with the lobes reflexed 5–8 mm higher. *Anther* 3–4 mm long, slightly longer than the free part of the filament.

Distribution — Solomon Islands; *Malesia*: eastern mainland New Guinea, Manus I., New Britain, New Ireland.

Habitat & Ecology — Mesic forests from 0 to 2230 m altitude; recorded hosts include *Calophyllum* and *Endiandra*.

4. *Sogerianthe sogerensis* (S. Moore) Danser

Sogerianthe sogerensis (S. Moore) Danser, Verh. Akad. Wet. Amst. Afd. Natuurk. 29 (1933) 106; Barlow, Austral. J. Bot. 22 (1974) 603; in Handb. Fl. Papua New Guinea 2 (1981) 252. — *Elytranthe sogerensis* S. Moore, J. Bot. 61, Suppl. (1923) 44. — Type: *Forbes* 715, New Guinea, Mt Woriwori. [For additional synonymy see Barlow, Austral. J. Bot. 22 (1974) 603].

Glabrous or the inflorescence and flower shortly and sparsely tomentose. *Leaves* opposite; lamina elliptic to ovate, 5–12 by 3–7 cm, cuneate at the base to a petiole 5–10 mm long, usually somewhat acuminate and acute to shortly rounded at the apex, dull on

both sides; venation distinct. *Inflorescences* several to many at the nodes; pedicel mostly 4–7 mm long and articulate above the middle, rarely obsolete; bracts 3, usually with two of these partly or completely fused and slightly imbricate with the third, 1–1.5 mm long, acute. *Corolla* in mature bud 25–35(–45) mm long, inflated below the middle, narrowed to a neck, weakly clavate and rounded or truncate at the apex, cream to red, sometimes darker above; tube in the open flower 12–18(–22) mm long with the lobes reflexed 4–6 mm higher. *Anther* 3–4 mm long, about equal to the free part of the filament. — **Fig. 42 c, d.**

Distribution — *Malesia*: New Guinea (mainland, eastern part), New Ireland.

Habitat & Ecology — Mesic forests from 0 to 1900 m altitude; recorded hosts include *Ficus*, *Kibara*, and *Mallotus*.

Note — On the New Guinean mainland the species is distinctive in the genus in its combination of long, articulate pedicel and small bracts. The specimens from New Ireland have a very short or obsolete pedicel, but otherwise agree with *Sogerianthe sogerensis*.

TAXILLUS

Taxillus Tiegh., Bull. Soc. Bot. France 42 (1895) 243. — Type species: *Taxillus tomentosus* (Roth) Tiegh., *T. ecurvus* (DC.) Tiegh., *T. bracteatus* (Wallich 1824, non Rich. 1792) Tiegh., syntypes.

Aerial stem-parasitic shrubs, more or less clothed in a tomentum of stellate hairs, slender to moderately robust, with epicortical runners bearing secondary haustoria. *Leaves* opposite. *Inflorescence* a simple few-flowered umbel; bract single under each flower, simple. *Corolla* 4- or 5-merous, gamopetalous, zygomorphic, with the tube curved prior to anthesis, deeply split on the inner side of the curve; lobes reflexed to the outer side at anthesis. *Anthers* basifixed, immobile. *Style* simple, with a knob-like stigma. *Fruit* ellipsoid. — **Fig. 43.**

Distribution — About 30 species in Africa, southern Asia from Pakistan to China, and southwards to Borneo. In *Malesia* 1 species.

Habitat & Ecology — Humid and open forests, from sea level to 3000 m; the species generally have broad host ranges.

Taxonomy & Phylogeny — The genus is related to *Dendrophthoe*, differing primarily in its umbellate inflorescence and the small more strongly zygomorphic flowers. For discussion of Afro-Asian origins, see Barlow (1990).

The genus is also closely related to, and difficult to delineate from the sympatric genus *Scurrula* (see note there).

Taxillus chinensis (DC.) Danser

Taxillus chinensis (DC.) Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 40. — *Loranthus chinensis* DC., Mém. Loran. (1830) 28. — Type: *Staunton*, China.

Loranthus sakoembangensis Korth., Verh. Bat. Genootsch. 17 (1839) 285. — Type: *Korthals s.n.*, Borneo, Mt Sakoembang.

Loranthus estipitatus Stapf, Trans. Linn. Soc., Bot. 4 (1894) 221. — *Taxillus estipitatus* (Stapf) Danser, Bull. Jard. Bot. Buitenzorg III, 10 (1929) 355. — Type: *Haviland 1351*, Borneo, Mt Kinabalu. [For further synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 40].

Young parts with a dense grey to dark brown or rarely paler indumentum of short stellate hairs, soon becoming sparse on adult stems and leaves and eventually on inflorescences and flowers. *Leaves* opposite; lamina elliptic to ovate, 2–4.5 by 1.5–3 cm, thin, cuneate at the base to a petiole 4–7 mm long, obtuse or rounded at the apex, dull on both sides or glossy above; venation pinnate with the midrib and major laterals visible above and prominent below. *Inflorescences* at the nodes, a 2-flowered umbel; peduncle (0.5–)1–6 mm long; pedicels 4–7 mm long; bract ovate, acute, 0.5–1 mm long. *Corolla* in mature bud 4-merous, (14–)22–32 mm long, slightly inflated at the base, slender above, strongly clavate and obtuse at the apex, greenish, often tinged yellow or brown, the colour somewhat obscured by the indumentum; tube (10–)15–22 mm long, split to the middle. *Anther* 1.5–2 mm long, about twice as long as the free part of the filament. *Fruit* 6–8 mm long, narrowly ellipsoid, warty, crowned by a collar c. 1 mm long. — **Fig. 43.**

Distribution — Burma to China and Vietnam; **Malesia:** Peninsular Malaysia, Borneo, northern Philippines.

Habitat & Ecology — Mesic and open forests, from 0 to 2700 m altitude but mostly at 600–1650 m; recorded hosts include *Acacia*, *Casuarina*, *Ficus*, *Litsea*, *Melastoma*, and *Scleropyrum*.

Notes — For discussion of status of *Taxillus estipitatus*, see Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 40. For discussion of conspecificity of *Loranthus sakoembangensis*, see Barlow, Blumea 36 (1991) 83.



Fig. 43. *Taxillus chinensis* (DC.) Danser. Twig with flowers and fruits (*Ramos 1112*). Redrawn from Danser (1931). Scale bar represents 1 cm.

THAUMASIANTHES

Thaumasianthes Danser, Rec. Trav. Bot. Néerl. 30 (1933) 464. — Type species: *Thaumasianthes amplifolia* (Merr.) Danser.

Aerial stem-parasitic shrubs (haustorial structure unknown). *Leaves* opposite. *Inflorescences* axillary, a sessile involucrate head of 12–18 sessile flowers arranged mostly in triads on a short receptacle; involucre bracts decussate, each subtending a triad, imbricate, enclosing the developing flowers; bracts of the individual flowers usually 3, foliaceous and together enclosing the flower bud. *Corolla* 6-merous, gamopetalous, regular or nearly so. *Anthers* basifixed, immobile. *Style* simple, with a knob-like stigma. *Fruit* not known. — **Fig. 44.**

Distribution — Endemic to *Malesia*; one species known only from the Philippines.

Habitat & Ecology — Not recorded but probably confined to lowlands; ecology including host preferences unknown.

Morphology & Taxonomy — The triads of flowers in the inflorescence are apparently not the simple dichasia which occur in other genera. Each individual flower is subtended by three bracts, as in *Macrosolen*, and may therefore represent a reduced true dichasium. The whole inflorescence, with its foliaceous involucre bracts subtending the false triads, may therefore be a condensed complex branching system. Since the true units of the inflorescence are single flowers with three bracts, and not simple triads, the relationship of *Thaumasianthes* is probably with *Lepidaria* rather than with *Lepeostegeres*. However, its unique inflorescence structure confirms Danser's recognition of *Thaumasianthes* as a distinct and isolated genus.

Conservation status — The genus is known from only 4 collections in a limited area, the last made in 1923.

Thaumasianthes amplifolia (Merr.) Danser

Thaumasianthes amplifolia (Merr.) Danser, Rec. Trav. Bot. Néerl. 30 (1933) 465. — *Loranthus amplifolius* Merr., Philipp. J. Sc., Bot. 13 (1918) 277. — Type: *Ramos BS 17448*, Samar.

Loranthus ovibracteatus Merr., Philipp. J. Sc., Bot. 13 (1918) 278. — *Thaumasianthes ovibracteata* (Merr.) Danser, Rec. Trav. Bot. Néerl. 30 (1933) 466. — Type: *Ramos BS 24135*, Samar.
[For additional synonymy see Danser, Rec. Trav. Bot. Néerl. 30 (1933) 466].

Glabrous. *Leaves* opposite; lamina ovate to broadly ovate, 12–20 by 6–15 cm, cuneate to truncate at the base to a winged petiole 6–16 mm long, acute or obtuse at the apex, slightly lustrous above or dull on both sides; venation pinnate with the midrib distinct above and raised and dark coloured below and the main laterals distinct on both sides. *Inflorescences* at the nodes, a sessile involucrate capitulum of 12–18 flowers arranged in triads; involucre 15–20 mm long, comprising 4 to 5 pairs of bracts and many lateral bracts which enclose the individual flowers, the longest outer ones elliptic to broadly cuneate, truncate to acute, smooth or keeled; floral axis c. 4 mm long; lateral bracts enclosing the flowers 7–11 mm long, keeled, acute. *Corolla* in mature bud 6-me-

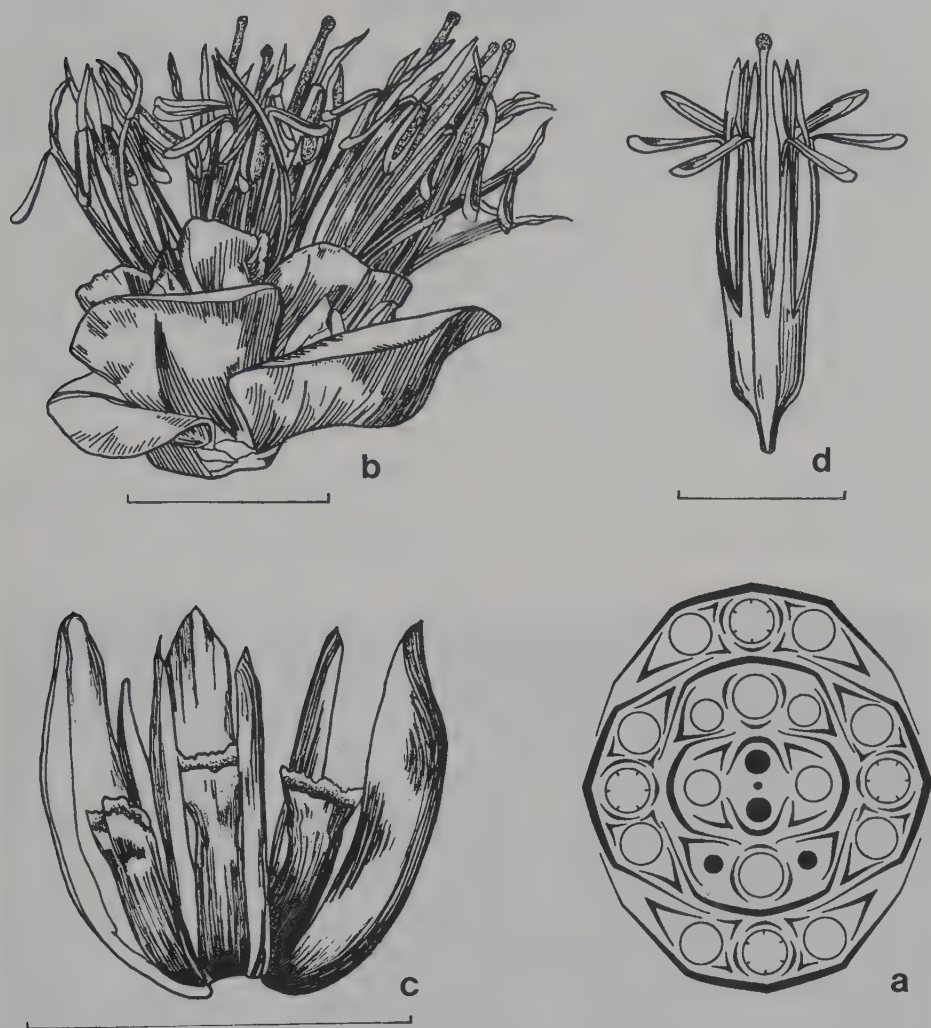


Fig. 44. *Thaumasianthes*. a. Generalized diagram of inflorescence. — *T. amplifolia* (Merr.) Danser. b. Inflorescence; c. triad in early fruiting stage; d. corolla, style and stamens (Collection not cited). Redrawn from Danser (1933). Scale bars represent 1 cm.

rous, 18–21 mm long, inflated cylindric from just above the base, truncate at the apex, pink or red below, yellow or green above; tube in the open flower 5–6 mm long with the lobes reflexed c. 10 mm higher. *Anther* 2–2.5 mm long, acute, about 4 times as long as the free part of the filament. — **Fig. 44b–d.**

Distribution — *Malesia*: Philippines (Samar, Leyte).

Habitat & Ecology — Lowlands, otherwise unknown.

TRITHECANTHERA

Trithecanthera Tiegh., Bull. Soc. Bot. France 41 (1894) 597. — Type species: *Trithecanthera xiphostachya* Tiegh.

Kingella Tiegh., Bull. Soc. Bot. France 42 (1895) 250. — Type species: *Kingella scortechinii* (King) Tiegh.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 425, 426].

Aerial stem-parasitic shrubs, mostly glabrous, robust, with epicortical runners bearing secondary haustoria. *Leaves* alternate, opposite or verticillate. *Inflorescence* a robust many-flowered raceme or spike; axis with a non-flowerbearing part at the base or apex; bract single under each flower, simple. *Corolla* 6-merous, strongly gamopetalous, thick and woody, regular or slightly zygomorphic with the tube curved prior to anthesis, more or less deeply split on the inner side of the curve. *Anthers* basifixed, immobile. *Style* simple, with a knob-like stigma. *Fruit* ellipsoid to obovoid. — **Fig. 45–47.**

Distribution — Endemic to *Malesia*; 5 species in Peninsular Malaysia and Borneo.

Habitat & Ecology — Humid forests, mostly in lowland dipterocarp forest to 1000 m; one species in highlands, 1000–3000 m; host specificity is probably low.



Fig. 45. *Trithecanthera sparsa* Barlow. With spiderhunter (*Arachnothera*), a pollinator bird. Borneo, Sarawak, Lambir Hills Nature Reserve (Nagamasu 4755). Photo Takakazu Yumoto, 1992, with permission.

Morphology & Taxonomy — The racemose inflorescences and gamopetalous corollas indicate relationship to *Dendrophthoe*. The genus is probably a local differentiate with strong specialization for bird pollination. Remarkable are the long robust corollas, and in some species the coloured non-flowerbearing part of the inflorescence axis, which may be either distal or proximal to the flowers, and may provide a perch for pollinators (H. Nagamasu, personal communication).

KEY TO THE SPECIES

- 1a. Leaves alternate, opposite or scattered 2
- b. Leaves verticillate in whorls of 4 or more 3
- 2a. Leaves mostly alternate, petiolate; inflorescence axis c. 55 mm long, bearing c. 20 flowers; corolla yellow **3. *T. sparsa***
- b. Leaves opposite, sessile or nearly so; inflorescence axis 140–190 mm long, bearing 40 or more flowers; corolla red **4. *T. superba***
- 3a. Inflorescence axis 20–40 mm long **2. *T. scortechinii***
- b. Inflorescence axis more than 200 mm long 4
- 4a. Leaves in whorls of c. 8; inflorescence axis lacking a sterile tip; flowers yellow ..
..... **1. *T. flava***
- b. Leaves in whorls of 4; inflorescence axis with a sterile tip more than 150 mm long; flowers pink or red **5. *T. xiphostachya***

1. *Trithecanthera flava* Kosterm.

Trithecanthera flava Kosterm., New Crit. Malaysian Plants III, Sect. For. Pl. (1955) 21. — Type: *Kostermans 7566*, Borneo, Peak of Balikpapan.

Glabrous except for the inflorescence and flowers pale yellow-brown tomentose. *Leaves* in whorls of 7–9; lamina oblong, 22–40 by 7–9 cm, thick, attenuate at the base to a shortly winged petiole 25–40 mm long and 3–4 mm thick, acuminate and acute to shortly rounded at the apex, glossy or dull above and dull below; venation pinnate with the midrib distinct above and raised below and the main laterals obscure above and visible below. *Inflorescences* at the nodes, a raceme of 40–70 flowers densely crowded in several spiral rows; axis 220–320 mm long, 8–10 mm thick, with a non-flowerbearing basal part 170–220 mm long, lacking a non-flowerbearing prolongation; pedicels 1–3 mm long, 2–3 mm thick. *Corolla* in mature bud 100–150 mm long, c. 3 mm wide at the base and inflated to 6–10 mm wide above, thick in the lower part, thinner in the inflated part, yellow, sometimes orange above; tube in the open flower 80–125 mm long, with a single variable slit to about halfway, with the petals reflexed 12–20 mm below the apex. *Anther* c. 10 mm long, obtuse, about equal to the free part of the filament. —

Fig. 46a, b.

Distribution — *Malesia*: Borneo.

Habitat & Ecology — 150–650 m altitude; recorded hosts include *Dipterocarpus* and *Schima*.

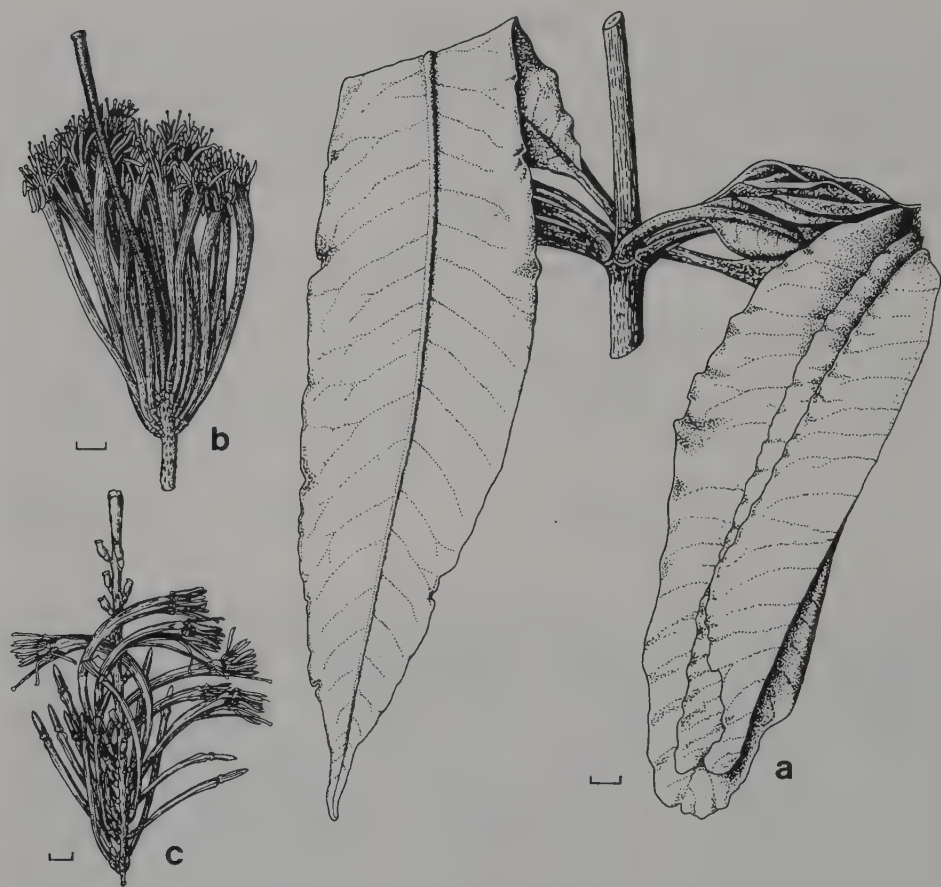


Fig. 46. *Trithecanthera flava* Kosterm. a. Portion of stem with leaves; b. inflorescence with some apical flowers fallen. — *T. superba* Danser. c. Inflorescence (a, b: *Kostermans* 7566; c: *Richards* 1652). a, b Redrawn from *Kostermans* (1955), c redrawn from *Danser* (1934). Scale bars represent 1 cm.

2. *Trithecanthera scortechinii* (King) Danser

Trithecanthera scortechinii (King) Danser, Verh. Kon. Akad. Wet. Amst. Afd. Natuurk. Sect. 2, 29 (1933) 128. — *Loranthus scortechinii* King, J. As. Soc. Beng. 56, ii (1889) 94. — Syntypes: *Scortechini* 90b, Perak; *Kunstler* 6020, Perak, Larut.

[For additional synonymy see *Danser*, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 426].

Glabrous. *Leaves* in whorls of 6; lamina narrowly ovate to oblong, 18–24 by 6–9 cm, cuneate or truncate at the base to a petiole 25–40 mm long, shortly attenuate and acute at the apex, dull on both sides; venation pinnate with the midrib distinct above and prominent below and the main laterals faintly visible on both sides. *Inflorescences* at the nodes, a raceme of many flowers in 6 spirals; axis 20–40 mm long, 3–4 mm thick, with a non-flowerbearing basal part 3–7 mm long, with a mucronate sterile tip c. 1 mm long; pedicels 1–1.5 mm long. *Corolla* in the mature bud 120–130 mm long, gradually widen-

ed upwards, narrowed to a neck in the upper part, clavate, angular and obtuse at apex, yellow below, green above; tube in the open flower 75–90 mm long with the lobes reflexed 5–8 mm higher. *Anther* 7–8 mm long, obtuse, about twice as long as the free part of the filament.

Distribution — *Malesia*: Peninsular Malaysia.

Habitat & Ecology — 30–240 m altitude; no hosts recorded.

3. *Trithecanthera sparsa* Barlow

Trithecanthera sparsa Barlow, *Blumea* 40 (1995) 29. — Type: *Chai S 34045*, Sarawak, Bukit Senkajang.

Glabrous. *Leaves* mostly alternate, rarely opposite or scattered; lamina ovate, 10–16 (–30) by 6–12 cm, thick, attenuate or cuneate at the base to a winged petiole 10–14 mm long, obtuse or rounded at the apex, dull on both sides; venation pinnate with the midrib visible above and prominent below and the main laterals obscure on both sides. *Inflorescences* at the nodes, a raceme (or spike) of 20–30 usually sparsely inserted flowers; axis 50–80 mm long, 4–6 mm thick, with a non-flowerbearing basal part 5–10 mm long, lacking a sterile tip; pedicels 0–1 mm long, c. 2 mm thick. *Corolla* in the mature bud 65–75 mm long, gradually widened upwards, with 2 rows of small wings near the point of reflexion of the lobes 18–25 mm below the apex, narrowed to a neck in the upper part, clavate and angular and obtuse at the apex, yellow with a green band at the neck and apex; tube in the open flower c. 55 mm long, more deeply split on one side, with the lobes reflexed 3–4 mm higher. *Anther* 8–10 mm long, obtuse, about twice as long as the free part of the filament. — **Fig. 45.**

Distribution — *Malesia*: Borneo.

Habitat & Ecology — Mixed dipterocarp forest from 400 to 1000 m altitude; the only recorded host is *Shorea*.

4. *Trithecanthera superba* Danser

Trithecanthera superba Danser, *Rec. Trav. Bot. Néerl.* 31 (1934) 245. — Type: *Richards 1652*, Borneo, Mt Dulit.

Glabrous. *Leaves* opposite; lamina oblong, 14–20 by 6–11 cm, truncate to slightly cordate at the base, sessile or subsessile, rounded or obtuse at the apex, dull on both sides; venation pinnate with the midrib and main laterals distinct above and only the midrib prominent below. *Inflorescences* at the nodes, a raceme of many flowers in oblique whorls; axis 140–190 mm long, 3–5 mm thick, with a non-flowerbearing basal part 25–50 mm long, lacking a sterile tip; pedicels 1–3 mm long, 1–2 mm thick. *Corolla* in the mature bud 60–95 mm long, gradually widened upwards, slightly winged and narrowed to a short neck in the upper part, cylindric and obtuse at the apex, red with a yellowish green band in the widest part; tube in the open flower 50–80 mm long, deeply split on one side, with the lobes reflexed 3–4 mm higher. *Anther* 7–10 mm long, obtuse, about twice as long as the free part of the filament. — **Fig. 46c.**

Distribution — *Malesia*: Borneo.

Habitat & Ecology — 1100–3000 m altitude; no hosts recorded.



Fig. 47. *Trithecanthera xiphostachya* Tiegh. Borneo, Mt Besar. Photo W. Forstreuter, 1989, with permission.

5. *Trithecanthera xiphostachya* Tiegh.

Trithecanthera xiphostachya Tiegh., Bull. Soc. Bot. France 41 (1894) 599. — Type: *Beccari 3148*, Sarawak, Batang Lupar.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 427].

Glabrous. *Leaves* in whorls of 4; lamina narrowly ovate to oblong, 20–30 by 8–11 cm, thick, truncate to slightly cordate at the base to a petiole 20–30 mm long, attenuate and acute at the apex, dull on both sides; venation pinnate with the midrib distinct above and prominent below and the main laterals faintly visible on both sides. *Inflorescences* at the nodes, a spike of many flowers in oblique whorls; axis 240–360 mm long, c. 10 mm thick at the base, thinner above, with a non-flowerbearing basal part 5–10 mm long, with a sterile tip 150–240 mm long. *Corolla* in the mature bud 120–150 mm long, gradually widened upwards, angular and narrowed to a short neck in the upper part, slightly clavate and obtuse at the apex, pink or red; tube in the open flower 75–105 mm long with the lobes reflexed 5–10 mm higher. *Anther* c. 15 mm long, obtuse, about 5 times as long as the free part of the filament. — **Fig. 47.**

Distribution — *Malesia*: Borneo.

Habitat & Ecology — 130–1000 m altitude; the only recorded host genus is *Pometia*, but hosts have been attributed to *Annonaceae*, *Guttiferae*, and *Myristicaceae*.

Note — Danser in Bull. Jard. Bot. Buitenzorg III, 10 (1929) 356 used the epithet *xiphostachys*, treating Van Tieghem's *xiphostachya* as an orthographic error. In view of Van Tieghem's Latin and Greek expertise, it is assumed that his use of the adjectival epithet was intentional, and it is followed here.

VISCACEAE

(B.A. Barlow, Canberra, Australia)¹

Viscaceae Batsch, Tab. Aff. Reg. Veg. (1802) 240, '*Viscinae*'; Miers, Contrib. Bot. (1851) 39, nom. provis.; Miq., Fl. Ind. Bat. 1, 1 (1856) 803; Agardh, Theoria Syst. Pl. (1858) 114; Tiegh., Bull. Soc. Bot. France 43 (1896) 247; Barlow, Proc. Linn. Soc. New S Wales 89 (1964) 269; Kuijt, Brittonia 20 (1969) 138. — *Loranthaceae* subfam. *Viscoideae* Engl., Nat. Pflanzenfam. 3, 1 (1889) 177; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 236. — Type genus: *Viscum* L.

[For additional synonymy see Barlow, Proc. Linn. Soc. New S Wales 89 (1964) 269].

Perennial evergreen or leafless plants, hemiparasitic on tree branches; attachment to the host by a single primary haustorium. *Stem* internodes terete or often angular or flattened, especially in species without developed leaves, often green. *Leaves* or their rudiments opposite, always simple; stipules absent. *Inflorescences* axillary or terminal; uniflorescence a simple cyme or a single flower, these sometimes aggregated to racemose or spicate compound inflorescences or expanded into dense clusters. *Flowers* small (mostly less than 2 mm long), monochlamydeous, unisexual; plants monoecious or (not in Malesia) dioecious. *Tepals* 2–4, valvate. *Stamens* as many as and opposite the tepals, epitepalous or free; anthers basifixed, free or sometimes united into a synandrium, 1- to many-celled, opening by pores or rarely slits; pollen spherical. *Ovary* inferior, 1-locular, with a short placental column; ovules absent; sporogenous cells located at the base of the placental column; stigma simple, sessile, nipple-like. *Fruit* berry-like, with a single seed covered by a sticky layer which develops in a zone internal to the vascular bundles.

DISTRIBUTION

Seven genera and about 400 species, predominantly tropical with fewer species in temperate regions. In *Malesia* 4 genera and 26 species, distributed throughout the region, without any distinct centre of species richness. For biogeography see below.

HABITAT

Mostly in tropical and warm temperate habitats; rare in seasonally cold temperate situations. In *Malesia* distributed through a range of forest habitats from lowland to tropic-subalpine at 3000 m altitude. They occur in all major forest types (everwet and seasonal, closed and open, humid and dry, primary and secondary, evergreen and deciduous).

An important element of habitat for *Viscaceae* is the host; see below for discussion of host specificity.

1) With contributions by P. Baas (leaf anatomy), R.W.J.M. van der Ham (palynology), and L. van den Oever (wood anatomy). Drawings adapted from various earlier publications and redrawn at CSIRO Plant Industry Visual Resources Unit, Canberra, principally by Sandie McIntosh, with contributions by Sue Percival and Carl Davies. Photographs are from different sources as indicated.

ECOLOGY

Like *Loranthaceae*, *Viscaceae* exhibit a suite of remarkable adaptations associated with the hemiparasitic habit; for additional details see under morphology below.

Except for *Korthalsella* and *Arceuthobium*, effective seed dispersal is by fruit-eating birds, and involves similar adaptations to those found in *Loranthaceae* (for details see there). In *Viscaceae* the fruits and seeds are usually smaller than those of *Loranthaceae*, but they have the same general architecture. In *Korthalsella* the fruits are mostly less than 2 mm long, and the minute seeds are released by a weak explosive mechanism (Stevenson 1934); dispersal is probably achieved by attachment to the feet or feathers of birds. In *Arceuthobium* a more powerful explosive mechanism propels projectile-shaped seeds considerable distances (Hinds et al. 1963; Hinds & Hawksworth 1965), and local dispersal from tree to tree is probably abiotic. See further discussion under plant geography.

Host preference and specificity vary widely within the family. Most *Viscaceae* grow on dicotyledonous hosts, but one genus (*Arceuthobium*) is specialized for and confined to coniferous hosts, and some species of *Dendrophthora*, *Korthalsella*, *Phoradendron* and *Viscum* also occur on conifers. In mixed forests with high tree species diversity many species of *Viscaceae* tend to have low host specificity, occurring on a broad range of host species; this is the case for several species in Malesia. However, other species show some specificity, including *Notothixos cornifolius*, which appears to have a strong host preference for species of *Sterculiaceae*. Also notable is the tendency for many species, especially of *Notothixos* and *Viscum*, to grow on other mistletoes, both of *Loranthaceae* and *Viscaceae*. The latter situation probably reflects the ease with which mistletoes can form haustorial attachments on related species, but may be adaptive in that it involves shared use of the same seed dispersal agents.

In open forests or woodlands with low tree species diversity the viscaceous flora tends to exhibit higher host specificity, sometimes involving differentiation of host races. Intraspecific variation or differentiation of host races in *Arceuthobium* and *Viscum*, for example, is linked with specificity for different hosts (Kuijt 1960; Wiens 1964; Hawksworth 1987; Nickrent & Stell 1990). In other cases, close adaptation for very unusual hosts occurs, for example in *Viscum minimum* of South Africa, which parasitizes succulent *Euphorbia* species, and in which only a fertile shoot c. 3 mm long emerges above the surface of the host (Wiens & Tölken 1979). *Viscum minimum* may thus be one of the smallest dicotyledons. High host specificity in *Viscaceae* is not generally associated with close visual resemblance to the preferred host, as occurs in some *Loranthaceae* (see there), although some species of *Phoradendron* closely resemble their preferred hosts in North America (Atsatt 1979).

The syndrome of floral characters indicates that pollination is consistently by insects. This contrasts with the adaptations of most *Loranthaceae*, which are predominantly bird pollinated. Pollinator guilds are unknown, at least for Malesia.

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A.L. Stell, *Biochem. Syst. Evol.* 18 (1990) 267–280. — Stevenson, G., *Trans. Roy. Soc. New Zealand* 64 (1934) 175–190. — Wiens, D., *Brittonia* 16 (1964) 11–54. — Wiens, D. & H.R. Tölken, *Fl. Southern Africa* 10 (1979) 1–59.

MORPHOLOGY

Haustorial system — The haustorial system in *Viscaceae* shows fewer primitive characters than that in *Loranthaceae* (see there). No species of *Viscaceae* are terrestrial root parasites, and none produce secondary haustoria on long epicortical runners. The absorbing connection to the host is therefore provided only by the primary haustorium developed on the embryo, although secondary sinkers to the host xylem may be produced from strands of tissue which spread in the cortex of the host (Gill & Hawksworth 1961). In some cases the primary haustorium becomes large and complex, with a convoluted contact surface and cortical strands. However, when species of *Viscaceae* parasitize other mistletoes the haustoria may be very simple and sometimes externally imperceptible.

Stems and leaves — In many species of *Viscaceae* the stems remain green, even in the case of leafy species. The stems are often sharply angular or flattened, both in leafy and leafless species. In genera in which both leafy and leafless species occur, habit and inflorescence characters suggest that the leafless state may have arisen many times, and it may therefore have a relatively simple genetic basis. The closest relatives of individual leafless species are usually leafy species, and sometimes such species pairs show few other differences.

Inflorescences — There are some parallel trends in inflorescence structure in *Viscaceae* and *Loranthaceae*, although inflorescences in the former family are generally less complex than in the latter. A common inflorescence unit widespread in *Viscaceae* is a simple dichasium (triad), although it is often amplified by sequential development of additional flowers in lateral positions, forming cymose fans or clusters, and sometimes it is reduced to a single flower. In monoecious species the individual cymules usually bear both male and female flowers, with the central flower (or flowers) being of one gender and the lateral flowers of the other; however, entirely female cymules are common in many species. In many cases the cymules are aggregated into larger conflorescences, which are mostly racemose or spicate.

Flowers and fruits — Ovary structure and embryology in *Viscaceae* are distinguished by some unusual features (Johri & Bhatnagar 1960). Comparable reductions in ovary structure occur in *Loranthaceae* (see there), but there are several differences which have been used to support distinction of *Loranthaceae* and *Viscaceae* as separate families (see below). There are no ovules, and the ovary shows very little internal differentiation. A small central placenta (mamelon) is present in *Arceuthobium*, *Korthalsella* and *Phoradendron*, but is much reduced or lacking in *Viscum*. Two to several sporogenous cells differentiate at the base of the mamelon. The embryo lacks a suspensor except in *Vis-*

cum, where it is very short. Normally only one embryo develops in the pseudoseed, and the viscous layer develops from a zone in the ovary wall internal to or within the vascular zone.

References: Gill, L.S. & F.G. Hawksworth, USDA Tech. Bull. 1242 (1961), 87 pp. (haustorial system). — Johri, B.M. & S.P. Bhatnagar, Proc. Nat. Inst. India 26B (1960) 199–220 (embryology).

VEGETATIVE ANATOMY

(P. Baas, leaf anatomy & L. van den Oever, wood anatomy)

Leaf anatomy — The leaf anatomy of Malesian *Viscum* is very poorly known. Stomata paracytic. Groups of silicified cells present in the mesophyll. Sclereid cells common (Engler & Krause 1935). Vascular bundles of the veins supported by arcs of collenchyma (Metcalf & Chalk 1950).

Wood anatomy — The description given below is based on literature data (Metcalf & Chalk 1950; Fahn et al. 1986) and original observations on three species. Only one of the specimens is from a tropical region and may be used as best reference for the Malesian area (*Viscum* sp., *Geesink* 7817, Thailand), the others are from Europe. Quantitative features given below are mainly restricted to the tropical specimen. The description must be considered as preliminary at best.

Growth rings faint to distinct. Vessels diffuse 20–30/mm², in radial multiples and solitary, tangential diameter up to 100 µm, vessel member length up to 350 µm; in the temperate species the vessel elements are very short (c. 100 µm) and storied together with the axial parenchyma strands. Perforations simple. Intervessel pits very small alternate, vessel-ray and vessel-parenchyma pits alternate, similar in shape and size to intervessel pits. Ground tissue composed of relatively thin-walled libriform fibres with minutely bordered pits mainly confined to the radial walls (in *Geesink* 7817), in the other specimens libriform fibres are scanty and the ground tissue is composed of vessel elements and axial parenchyma.

Parenchyma predominantly apotracheal, diffuse, partly scanty paratracheal, in strands of 2–5 cells.

Rays mainly uniseriate and heterocellular in the tropical specimen; in the other species up to 6-seriate and often compound.

Crystals solitary, infrequent in non-chambered ray or axial parenchyma cells.

References: Engler, A. & K. Krause, Loranaceae. Nat. Pflanzenfamilien, ed. 2, 16b (1935) 103–105. — Fahn, A., E. Werker & P. Baas, Wood anatomy and identification of trees and shrubs from Israel and adjacent regions (1986) 126–127; Israel Academy of Sciences. — Metcalf, C.R. & L. Chalk, Anatomy of the Dicotyledons 2 (1950) 1188–1194.

POLLEN MORPHOLOGY

(R.W.J.M. van der Ham)

Pollen of the *Viscaceae* is rather poorly known. Only that of *Viscum*, including four of the species occurring in Malesia, has been thoroughly described by Feuer & Kuijt (1982)

and Feuer et al. (1982). These studies contain scanning as well as transmission electron micrographs. Pollen of *Korthalsella* is dealt with in several regional accounts, e.g.: Madagascar: Muller et al. (1989); China: Liu & Qiu (1993); New Zealand: Moar (1993). The pollen of *Ginalloa* and *Notothixos* is unknown. The pollen morphology of the predominantly neotropical *Arceuthobium* was monographically studied by Hawksworth & Wiens (1996), but not published in a comprehensive way. Regional data were provided by Quiroz-García et al. (1986) and, including one of the Old World species, Liu & Qiu (1993). The pollen of the large exclusively neotropical genera *Dendrophthora* (Rizzini 1956) and *Phoradendron* (Quiroz-García et al. 1986) is very incompletely known.

In contrast to the pollen of most *Loranthaceae*, which is oblate and triangular, *Viscaceae* pollen is usually spheroidal to subprolate with a more or less rounded equatorial outline. Only that of African *Viscum* is often suboblate with a lobate outline. *Arceuthobium* pollen may be distinctly 6-lobate when the three pseudocolpi are invaginated. *Viscum* has the largest pollen grains in the family: largest diameter from 32 to 55 µm; that of other genera ranges from 17 to 33 µm. Except for a number of African *Viscum* species that show (3-) 4–6-aperturate grains, the pollen of *Viscaceae* is 3-aperturate. In one African *Viscum* species (5-) 7–10-rugorate pollen was found. The apertures are usually compound, though the ectoaperture is sometimes short and indistinct and the endoaperture not always well-defined. Simple, colpate apertures occur in a few African *Viscum* species and possibly all *Arceuthobium* species. Pseudocolpi are present in *Arceuthobium* and a few *Viscum* species (Feuer & Kuijt 1982: fig. 14; Feuer et al. 1982: fig. 1–3, 37, 60). Exine ultrastructure has been studied in *Viscum*. The exine is 3-layered (tectum, infratectum, nexine). An endexine is present throughout the grain. The infratectum is finely granular, or granular at the poles and columellate in the equatorial parts, or columellate throughout. The tectum is nearly closed, sometimes very thin or restricted to 'supratectal' elements. Ornamentation in *Viscaceae* pollen is either psilate to scabrate or verrucate (*Dendrophthora*, *Korthalsella*, *Phoradendron*, *Viscum*), sometimes supracreticulate (*Viscum*), or more or less echinate, showing a loose to dense cover of usually conical pointed elements (*Arceuthobium*, *Viscum*). The four *Viscum* species occurring in Malesia (Feuer & Kuijt 1982) all have scabrate/verrucate pollen; the nearest echinate *Viscaceae* pollen reported is that of *V. alniformosanae* from Taiwan (Feuer & Kuijt 1982) and *A. chinense*, *V. coloratum* and *V. nudum* from China (Liu & Qiu 1993).

According to Feuer et al. (1982) the basic characters of *Viscum* pollen are subprolate, rounded equatorial outline, 3-colporate aperture system, non-uniform columellate/granular exine structure and non-uniform non-prominent ornamentation, which features are all represented in Asian *Viscum*. Due to the lack of detailed data of the other genera no intrafamilial relationships can be established on the basis of pollen morphology. There is no clear relationship between the pollen of *Viscaceae* and *Loranthaceae*. The *Viscaceae* do share a number of characters with the *Eremolepidaceae*: 3-colporate aperture system, exine structure (finely granular infratectum) and echinate ornamentation (Feuer & Kuijt 1978).

Fossil pollen that might be assigned to the *Viscaceae*, and much alike that of the extant *Arceuthobium oxycedri*, was described as *Spinulaepollis arceuthobiodes* from early

Eocene to Pliocene strata in central Europe (Muller 1981: *Arceuthobium* type). Hawksworth & Wiens (1972) listed Miocene to Holocene finds of *Arceuthobium* pollen from North America and later added further details on records from Europe, Asia and North America, from Eocene to Holocene (Hawksworth & Wiens 1996). Selling (1947) recorded *Korthalsella* pollen from the Holocene of Hawaii. Fossil *Viscum* pollen is known from the Pliocene of the Netherlands and Germany (Muller 1981).

References: Feuer, S.M. & J. Kuijt, Can. J. Bot. 56 (1978) 2853–2864; Amer. J. Bot. 69 (1982) 1–12. — Feuer, S.M., J. Kuijt & D. Wiens, Amer. J. Bot. 69 (1982) 163–187. — Hawksworth, F.G. & D. Wiens, Biology and classification of dwarf mistletoes (*Arceuthobium*). USDA Agric. Handb. (1972) 401; Dwarf mistletoes: biology, pathology and systematics. USDA Agric. Handb. (1996) 709. — Liu, L.F. & H.X. Qiu, Guihaia 13 (1993) 235–245. — Moar, N.T., Pollen grains of New Zealand dicotyledonous plants (1993). — Muller, J., Bot. Rev. 47 (1981) 1–142. — Muller, J., M. Schuller, H. Straka & B. Friedrich, Trop. Subtrop. Pflanzenwelt 67 (1989) 5–17. — Quiroz-García, D.L., R. Palacio-Chávez, M. de la Luz Arreguín-Sánchez & D. Ramos-Zamora, Phytologia 60 (1986) 373–382. — Rizzini, C.T., Rodriguésia 30/31 (1956) 87–234. — Selling, O.H., Spec. Publ. B.P. Bishop Mus. 38 (1947).

CHROMOSOMES.

Chromosomal characters have made a significant contribution to phylogenetic knowledge of the family, especially in relation to the origin and maintenance of dioecy in *Viscum*. The primary basic chromosome number is $x = 14$, and the other basic numbers of $x = 15, 13, 12, 11$ and 10 indicate progressive dysploid increase or reduction, usually within genera (Wiens & Barlow 1971, 1979). Polyploidy is rare, but some species have very large chromosomes, the largest equalling those of *Loranthaceae* and any others in the plant kingdom.

In *Viscum* sex-associated and floating chromosome translocation complexes are characteristic of dioecious species, but are virtually absent in monoecious species (Wiens & Barlow 1979; Barlow 1981; Aparicio 1993). This suggests that the translocations are primarily associated with the origin and establishment of dioecy, by bringing non-allelic male- and female-determining factors into genetic linkage. The inception of dioecy appears to have initiated a significant secondary radiation of *Viscum*, especially in Africa (Barlow 1983).

References: Aparicio, A., Bot. J. Linn. Soc. 111 (1993) 359–369 (sex-associated translocations). — Barlow, B.A., Bot. Mag. Tokyo 94 (1981) 21–34 (sex-associated translocations, dioecy); in D.M. Calder & P. Bernhardt (eds.), The Biology of Mistletoes (1983) 19–46, Academic Press. — Wiens, D. & B.A. Barlow, Taxon 20 (1971) 313–332 (karyology); Heredity 42 (1979) 201–222 (karyology, dioecy).

PHYTOCHEMISTRY AND CHEMOTAXONOMY

Much of the phytochemical study of mistletoes has been undertaken at a time when the *Loranthaceae* and *Viscaceae* were treated as a single family *Loranthaceae* sens. lat. Furthermore many of the studies have involved comparative work in several genera of both families, identifying similarities and differences between the groups then considered subfamilies. For this reason the phytochemistry of the two families has been considered together, to identify the contribution of chemotaxonomy to the current treatment of the

two families. As might be predicted, phytochemical studies have shown a number of shared features between the two families. However they have also revealed significant differences which support their distinction. For details see the introductory section on phytochemistry and chemotaxonomy for the family *Loranthaceae* (p. 217).

USES

Mistletoes, including *Viscaceae*, feature prominently in folk legend and medicine (Kanner 1939; Barlow 1987). For general discussion, see introduction to *Loranthaceae*. The traditional European mistletoe *Viscum album* is prominent in mythology, for which it has an extensive literature. The Golden Bough of classical Roman mythology was probably this species, as was the killer of the sungod, Balder, of the Germanic peoples, and the heavenly plant worshipped by the Celts. Some of the beliefs surrounding European mistletoe have been transferred to *Phoradendron* in the New World.

A detailed review of uses of mistletoes (primarily *Viscaceae* but also *Loranthaceae*) was provided by Kanner (1939). Along with many magical uses are therapeutic applications which appear to reflect genuine properties of the plants. Institutes which focus specifically on researching medicinal properties of *Viscum album* have been established, with a strong emphasis on cancer research; for brief historical summaries and experimental studies see, for example, Sallé (1980) and Hülsen & Mechelke (1982).

References: Barlow, B.A., *Biologist* 34 (1987) 261–269. — Hülsen, H. & F. Mechelke, *Arzneim.-Forsch. Drug Res.* 32 (1982) 1126–1127. — Kanner, L., *Bull. Hist. Med.* 7 (1939) 875–936. — Sallé, G., *Planta Medica* 38 (1980) 43–49.

TAXONOMY

General acceptance of *Viscaceae* as a family distinct from *Loranthaceae* dates from about 1960. As early as 1802 Batsch distinguished the group at this level, and was followed by Miers, Miquel, Agardh and Van Tieghem. Other influential authors, including Engler, Danser and Krause relegated the group to subfamily rank within *Loranthaceae*. More recent sources of data supporting distinction at family level include embryology (Johri & Bhatnagar 1960; Dixit 1962), karyology (Barlow 1964; Wiens & Barlow 1971) and morphology (Kuijt 1968, 1969). The brief diagnostic key to the two families presented at the end of this section covers all Malesian taxa.

Further to the strong grounds for treating *Viscaceae* as a family distinct from *Loranthaceae*, there is some evidence that the two families may not even be directly related (Kuijt 1968). Some genera of *Santalaceae* and *Olcaceae* also show reductions in ovary structure, and aerial stem parasitism also occurs in other families of *Santalales*. Some of the striking features of haustorial structure, ovary structure and growth habit in *Loranthaceae* and *Viscaceae* may therefore be parallel developments (and divergent specializations) acquired from different direct ancestors in *Santalales* (possibly in *Olcaceae* and *Santalaceae* respectively), so that their common ancestor may be phylogenetically more remote.

Within the *Viscaceae* generic limits have remained relatively stable. However, there is no consensus on the relationships between all genera and their arrangement into subfamilies or tribes. In contrast to *Loranthaceae*, karyology provides little useful data. Various inflorescence and floral characters have been applied in assessing relationships between genera, but differences in weighting lead to different arrangements. Because of the small number of genera in the family, and their obvious affinities with each other, there seems little merit in establishing subfamilial taxa, and none are utilized here.

At the species level there are difficulties in several genera. Many species show considerable morphological variability, some of which may be responses to different growing conditions. In Malesia the greatest difficulties are in *Korthalsella*, for which Molvray (1990) has argued a substantial reduction in the number of species recognized by Danser (1937, 1940), and in *Viscum*, in which apparently widespread species show considerable polymorphism. Like *Loranthaceae*, narrow species concepts in the past have led to segregate taxa being recognized. For Malesia many names have been placed in synonymy, especially by Danser (1931, 1935, 1937, 1940, 1941).

Phylogenetic analysis of *Viscaceae* is difficult, owing to uncertainties about generic relationships, and to the limited number of characters for which polarity states are evident, and applicable at the generic or natural group level. A possible phylogenetic relationship of the genera is indicated by the biogeography of the family (see below).

KEY TO THE FAMILIES

- 1a. Perianth monochlamydeous, with tepals mostly less than 2 mm long; flowers unisexual, with male and female flowers usually in the same inflorescence; pollen spherical; fruit with the viscous layer inside the vascular bundles; embryo suspensor very short or absent **Viscaceae**
- b. Perianth dichlamydeous, with the calyx reduced to a limb at the apex of the ovary and the corolla (2.5–)10–150 mm long; flowers mostly bisexual, rarely functionally unisexual and then with vestigial organs of the other sex present and plants mostly dioecious; pollen trilobate; fruit with the viscous layer outside the vascular bundles; embryo suspensor long, multiseriate **Loranthaceae** (p. 209)

References: Barlow, B.A., Proc. Linn. Soc. New S Wales 89 (1964) 268–272 (family status). — Danser, B.H., Bull. Jard. Bot. Buitenzorg III, 11 (1931) 233–519; 14 (1937) 115–159; 16 (1940) 329–342; Philipp. J. Sc. 58 (1935) 1–128; Blumea 4 (1941) 261–319 (all taxonomy). — Dixit, S.N., Bull. Bot. Surv. India 4 (1962) 49–55 (embryology). — Johri, B.M. & S.P. Bhatnagar, Proc. Nat. Inst. Sci. India 26B (1960) 199–220 (embryology). — Kuijt, J., Brittonia 20 (1968) 136–147 (family status); The biology of parasitic flowering plants (1969), Univ. California Press (family status). — Molvray, M., PhD Thesis, Tulane Univ., Louisiana, USA (1990), 159 pp. — Wiens, D. & B.A. Barlow, Taxon 20 (1971) 313–332 (karyology).

PLANT GEOGRAPHY

Because of the nature of seed dispersal mechanisms in most genera of *Viscaceae*, their dispersability is normally very low. With the striking exception of *Korthalsella*, the family has a strongly continental distribution, and the present distribution of the family has

probably been achieved largely by migration over continuous land surfaces. This allows confidence in the correlation of area, migration and phylogeny. *Korthalsella* is remarkable among all mistletoes for its wide distribution to, and diversification on, remote oceanic islands, perhaps attributable to dispersal of the minute seeds on the feet and feathers of migratory birds rather than by ingestion. Determining the centre of origin of *Korthalsella* is therefore difficult, and contributes little to an analysis of the entire family.

At least four of the seven genera of *Viscaceae* appear to be centred in the southeast Asian/Malesian region (Barlow 1983). A fifth genus, *Arceuthobium*, whilst species-rich in North America, is probably Asian in origin (Hawksworth & Wiens 1972, 1996). An eastern Asian origin for *Viscaceae* has therefore been postulated (Barlow 1983), with *Arceuthobium*, *Dendrophthora* and *Phoradendron* reaching the New World via the Tertiary Beringian land connection, associated at least in part with migration of the preferred hosts. The family may ultimately be of Gondwanan origin (Barlow 1990), but its major diversification was probably a Tertiary palaeotropical Laurasian event.

All four genera of *Viscaceae* in Malesia are centred there or in Southeast Asia, and show some attenuation across Charles's Line to Papuasia, Australia and the Pacific. They are probably all components of the one floristic element, a tropical one with a primary centre in SE Asia, which has diversified in the Malesian region (up to generic level), and which is represented further southeastwards in Australia only as an intrusive stock.

References: Barlow, B.A., in D.M. Calder & P. Bernhardt (eds.), *The Biology of Mistletoes* (1983) 19–46, Acad. Press; in P. Baas et al. (eds.), *The Plant Diversity of Malesia* (1990) 273–292, Kluwer Academic Publ. — Hawksworth, F.G. & D. Wiens, *Biology and classification of dwarf mistletoes (Arceuthobium)*. USDA Agric. Handb (1972) 401; *Dwarf mistletoes: biology, pathology and systematics*. USDA Agric. Handb. (1996) 709.

KEY TO THE GENERA

- 1a. Plants leafy 2
- b. Plants lacking normally developed leaves 3
- 2a. Plants densely white to golden or brown stellate-hairy, especially on the young parts **Notothixos** (p. 425)
- b. Plants glabrous or nearly so 4
- 3a. Flowers minute (mostly less than 0.5 mm long); anthers 3, fused into a single unit; fruits up to 3 mm long; [in Malesia plants mostly less than 20 cm long; internodes in most species flattened in the one plane to form a cladode] . **Korthalsella** (p. 418)
- b. Flowers small (mostly 0.5–2 mm long); anthers 3 or 4, free from each other; fruits more than 3 mm long; [in Malesia plants mostly reaching more than 30 cm length; internodes in most species terete or when angular or flattened with the succeeding ones at right angles] 4
- 4a. Inflorescence a spike of decussate single flowers or 3-flowered cymes; anthers opening by slits; tepals persistent on the fruit **Ginalloa** (p. 412)
- b. Inflorescence a single 3- or 5-flowered cyme, sometimes with subsidiary cymes or flowers arising within or below the first; anthers opening by several pores; tepals not persistent on the fruit (except in *V. loranthi*) **Viscum** (p. 432)

GINALLOA

Ginalloa Korth., Verh. Bat. Genootsch. 17 (1839) 260. — Type species: *Ginalloa arnottiana* Korth.

Aerial stem-parasitic shrubs, glabrous. *Stems* much-branched, striate or longitudinally wrinkled. *Leaves* opposite, with normally developed ones and rudimentary cataphyll-like ones borne on each branch; normally developed leaves entire, unifacial, curvined, with 1–5 veins usually visible on both surfaces; rudimentary leaves forming a boat-shaped collar encircling the stem. *Inflorescences* terminal and axillary, a spike of decussate pairs of cymules (triads) or single flowers; central flowers usually female; lateral flowers female or male; bracts small, in pairs forming a boat-shaped cupule (like the rudimentary leaves) subtending each cymule; bracteoles of the lateral flowers (when present) small, free, entire to densely fimbriate. *Male flowers* globose or somewhat flattened, 0.5–1 mm long, 3-merous; tepals triangular, valvate; anthers disc-shaped, 2-loculate, opening by slits, on a short filament. *Female flowers* cylindric or narrowly ellipsoid, at anthesis usually less than 2 mm long, usually 3-merous; tepals triangular; stigma small, nipple-shaped. *Fruit* narrow-ellipsoid to ellipsoid, smooth or tuberculate, crowned by the persistent tepals. — **Fig. 1, 2.**

Distribution — Perhaps 9 species distributed from Sri Lanka eastwards and southwards to New Guinea and Solomon Islands. In *Malesia* 6 species, without a distinct centre of diversity.

Habitat & Ecology — Mostly in closed humid forests but extending to open woodlands and disturbed habitats, common in lowlands but extending to 2100 m altitude in New Guinea. Host specificity is low.

Morphology — In most species of *Ginalloa* the stems long remain green. *Ginalloa* is similar to *Notothixos* in producing both normally developed and rudimentary cataphyll-like leaves on each branch system but in *Ginalloa* the pattern is more variable, and some species bear very few normal leaves.

The basic inflorescence unit is a small 3-flowered dichasium (cymule), usually with both male and female flowers, although all-female cymules are sometimes produced when flowering is prolific. The spicate arrangement of the cymules is consistent in the genus *Ginalloa*, although in several species the cymules are often or always reduced to solitary flowers.

Phylogeny — *Ginalloa* is probably the least specialized genus of *Viscaceae*. It shows clear links to each of the other three genera in Malesia, supporting the view that Malesia may be a major centre of diversification for the family (see phytogeography discussion above).

Taxonomy — There is no critical revision of the entire genus, and the taxonomic status of species from Burma and the Andaman Islands is uncertain.

KEY TO THE SPECIES

- | | |
|--|---|
| 1a. Inflorescence up to 10 mm long; cymules mostly 1-flowered | 2 |
| b. Inflorescence more than 10 mm long; cymules mostly 3-flowered | 3 |

- 2a. Plants with normally developed and rudimentary leaves in successive pairs; normal leaves 5–40 mm long; inflorescences mostly terminal, with 3–16 pairs of cymules **4. *G. linearis***
- b. Plants seemingly sparsely leafy or leafless, with rudimentary leaves produced at most or all nodes; normal leaves 30–50 mm long; inflorescences mostly axillary, mostly with 2 or 3 pairs of cymules **5. *G. nuda***
- 3a. Bracteoles densely fimbriate, forming a tuft of white hairs surrounding the flowers; spikes 80–200 mm long with internodes 8–20 mm long; fruit white **3. *G. flagellaris***
- b. Bracteoles entire or serrate; spikes 20–90 mm long with internodes 2–7 mm long; fruit yellow to red **4**
- 4a. Normal leaves linear to narrowly lanceolate, less than 10 mm wide **1. *G. angustifolia***
- b. Normal leaves narrowly to broadly ovate or elliptic, more than 10 mm wide ... **5**
- 5a. Normal leaves thickly coriaceous, broadly elliptic or broadly ovate; rudimentary leaves 2–4 mm above each leafy node, ragged at the margin; spikes 20–35 mm long with 8–10 pairs of cymules **6. *G. siamica***
- b. Normal leaves thinly coriaceous, narrowly ovate to ovate; rudimentary leaves mostly 7–25 mm above each leafy node, entire at the margin; spikes 30–90 mm long with 9–40 pairs of cymules **2. *G. arnottiana***

1. *Ginalloa angustifolia* (Merr.) Danser

Ginalloa angustifolia (Merr.) Danser, Philipp. J. Sc. 58 (1935) 132. — *Ginalloa cumingiana* var. *angustifolia* Merr., Philipp. J. Sc., Bot. 4 (1909) 153. — Type: *Banks BS 1139*, Negros.

Plant slender, probably pendulous, to 0.6 m long. *Stems* with rudimentary leaves on each growth segment; internodes terete, (7–)25–40 mm long, 0.5–2 mm in diameter. *Leaves* rudimentary and normally developed in successive pairs; normally developed leaves linear to narrowly lanceolate, often falcate, attenuate at the base to an obscure petiole 2–4 mm long, attenuate and finally shortly rounded at the apex, 3-nerved, with veins visible on both sides, 40–60 by 2–8 mm; rudimentary leaves (7–)10–25 mm above each leafy node, c. 0.5 mm high. *Inflorescences* commonly terminal, often in threes, sometimes axillary, 10–40 mm long, a spike of 4–10 pairs of triads or single flowers; internodes 2–7 mm long; bracteal cup c. 1 mm long; bracteoles acuminate, serrate, 0.4–0.8 mm long. *Fruit* ellipsoid, smooth or slightly rugose, orange or red.

Distribution — *Malesia*: Philippines (Luzon, Negros, Palawan).

Habitat & Ecology — 0–1300 m altitude; only recorded host *Garcinia*.

Note — Closely related to *G. arnottiana*, differing in the narrow, more or less falcate 3-veined leaves shortly rounded at the apex and the shorter inflorescence. Also similar to *G. spathulifolia* of Sri Lanka, differing in the cataphyll-like rudimentary leaves being less consistently positioned near the stem bases, smaller persistent tepals on the fruits and shorter more sharply differentiated inflorescences.

2. *Ginalloa arnottiana* Korth.

Ginalloa arnottiana Korth., Verh. Bat. Genootsch. 17 (1839) 260; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 449; Philipp. J. Sc. 58 (1935) 130. — Type: *Korthals s.n.*, Borneo, Kalimantan, Tandjoeng Djawa.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 449; Philipp. J. Sc. 58 (1935) 130].

Plant slender to moderately robust, erect, 50–80 cm in diameter. *Stems* usually with rudimentary leaves on each growth segment; internodes terete or slightly dilated and flattened upwards, (2–)15–80 mm long, 1–3 mm in diam. *Leaves* usually rudimentary and normally developed in successive pairs; normally developed leaves narrowly ovate to ovate or elliptic, attenuate at the base to an obscure petiole 2–8 mm long, often undulate at the margin, more or less acuminate and finally shortly rounded at the apex, 3-nerved, with veins visible on both sides, 40–90(–110) by 10–30 mm; rudimentary leaves rarely lacking, rarely in two successive pairs, (2–)7–25 mm above each leafy node, c. 1 mm high. *Inflorescences* commonly terminal, often in threes, sometimes axillary, 30–90 mm long, a spike of 9–25(–40) pairs of triads or sometimes single flowers; internodes 2–5 mm long; bracteal cup c. 0.5 mm long, spreading; bracteoles acuminate, almost entire to serrate, rarely (not in Malesia) densely fimbriate, 0.4–1 mm long. *Fruit* narrowly ellipsoid to ellipsoid, smooth or rarely finely verrucose, yellow to red. — **Fig. 1a.**

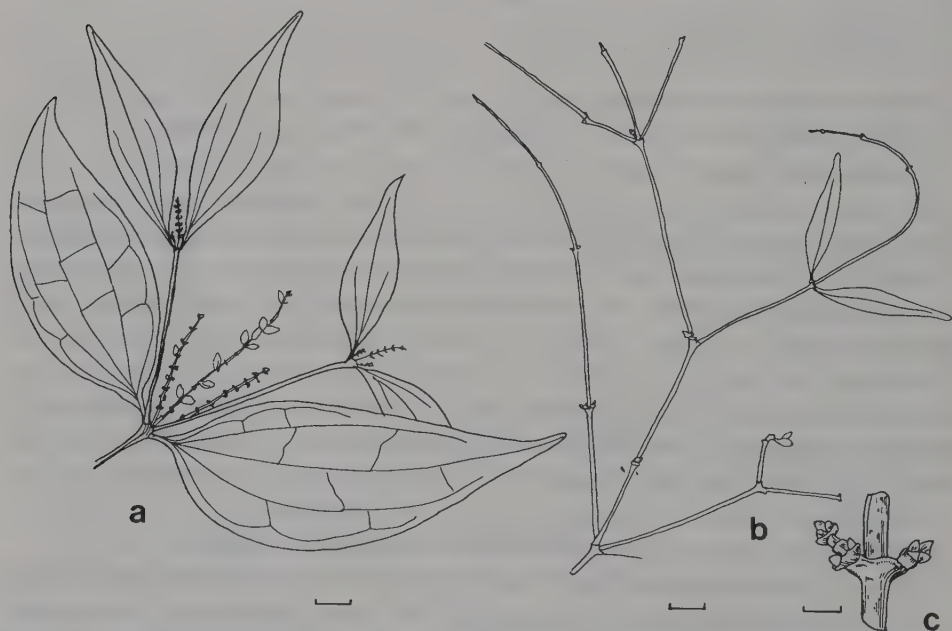


Fig. 1. *Ginalloa arnottiana* Korth. a. Twig with inflorescences. — *G. nuda* Danser. b. Habit; c. inflorescences (a: Winkler 2437; b, c: Clemens 31538). Redrawn from Danser (1931, 1934). Scale bars represent 1 cm (a, b), resp. 1 mm (c).

Distribution — Solomon Islands; *Malesia*: Borneo, Philippines, Celebes, Lombok, Moluccas. See note on disjunct distribution.

Habitat & Ecology — Primary and secondary humid forests and disturbed sites, from 0 to 2100 m altitude; recorded hosts include *Citrus*, *Eugenia*, *Mallotus*, *Mitrephora*, *Parinari*, *Schima*, *Shorea*.

Note — There is a striking disjunction in the species area between the Moluccas and the Solomon Islands, with the intervening area in New Guinea occupied by *G. flagellaris* (see note there). In the Solomon Islands *G. arnottiana* shows the strongly fimbriate bracteole character which is otherwise diagnostic of *G. flagellaris*.

3. *Ginalloa flagellaris* Barlow

Ginalloa flagellaris Barlow, Blumea 41 (1996) 339. — Type: Womersley & Whitmore NGF 19070, Papua New Guinea, Wau.

Ginalloa arnottiana auct. non Korthals: Danser, Blumea 3 (1938) 54.

Plant slender to moderately robust, pendulous, to 0.6 m long. *Stems* with rudimentary leaves on each growth segment; internodes terete, 20–60 mm long, 1–3 mm in diam. *Leaves* mostly rudimentary or sometimes rudimentary and normally developed in successive pairs; normally developed leaves often falling early, narrowly to broadly elliptic, attenuate or cuneate at the base to an obscure petiole 5–10 mm long, attenuate to acuminate and acute at the apex, 5-nerved, with veins visible on both sides, 80–160 by 25–60 mm; rudimentary leaves 0.8–1.5 mm high. *Inflorescences* commonly terminal, often in threes, also axillary, often branching near the base, often not strongly differentiated from vegetative stems, 80–200 mm long, a spike of 15–25 pairs of triads; internodes 8–15 (–20) mm long; bracteal cup c. 1 mm long, spreading; bracteoles densely fimbriate, forming a tuft of white hairs surrounding the flowers. *Fruit* ellipsoid, smooth, white. —

Fig. 2.

Distribution — *Malesia*: New Guinea, New Britain.

Habitat & Ecology — Humid forests from 400 to 1860 m altitude; *Garcinia* is a commonly recorded host; others include *Antidesma*, *Castanopsis*, *Vavaea*.

Note — Geographically replaces *G. arnottiana*, from which it is possibly derived but distinct in several characters, including larger and fewer normally developed leaves not undulate, longer inflorescences and inflorescence segments, and especially the white fruits. *Ginalloa flagellaris* is also distinct in its densely fimbriate bracteoles, forming a tuft of white hairs surrounding the flowers; the occurrence of this character in *G. arnottiana* in the Solomon Islands may be a result of introgression.

4. *Ginalloa linearis* Danser

Ginalloa linearis Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 451. — Type: Hallier B3049, Borneo, Kalimantan, Liang Gagang.

Ginalloa applanata Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 448. — Type: Hallier B1780, Borneo, Kalimantan, Mt Kenepai.

[*Ginalloa tenuifolia* Tiegh., Bull. Soc. Bot. France 42 (1895) 647, nom. nud. — Types: Beccari 1971 & 2348, Borneo].

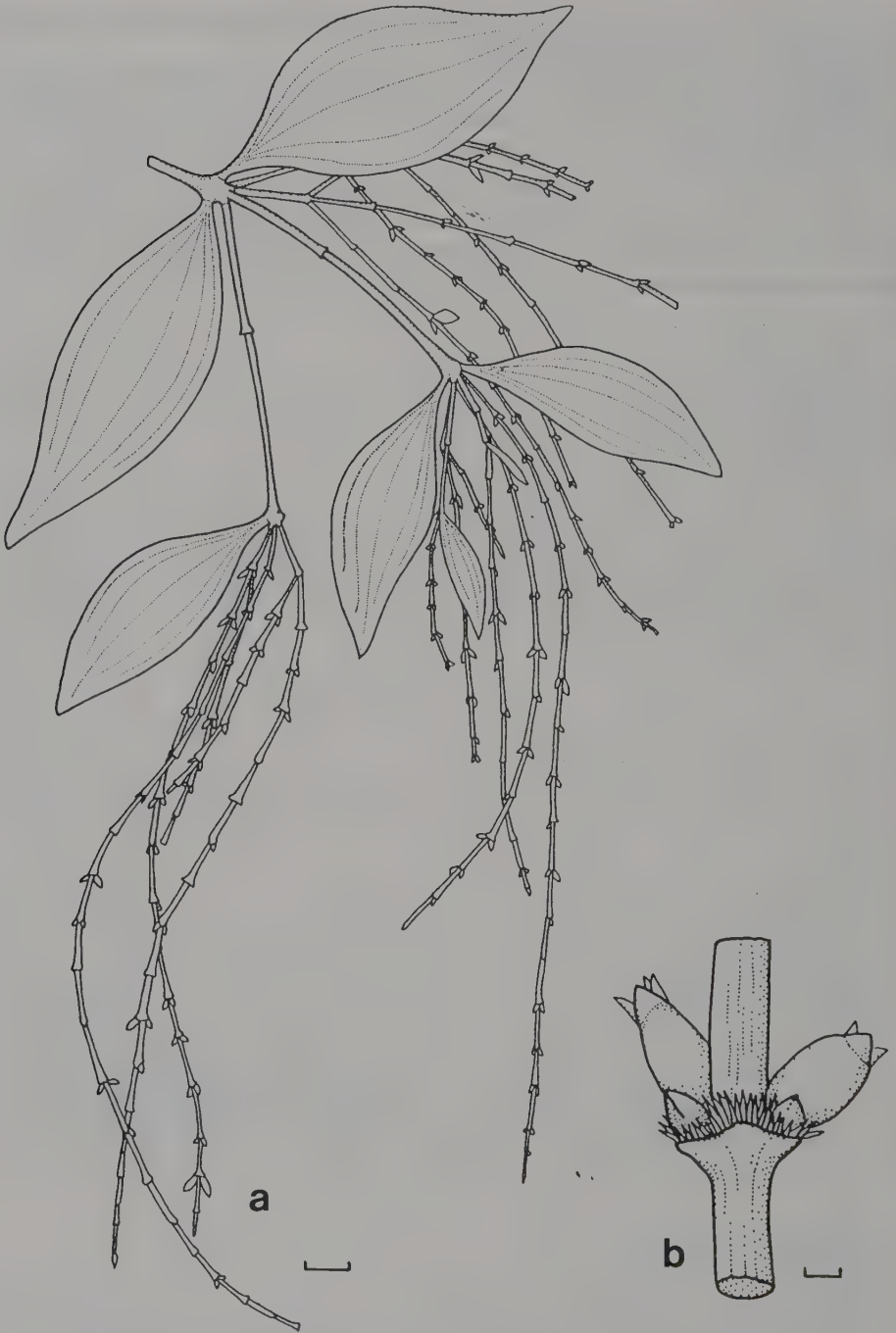


Fig. 2. *Ginallia flagellaris* Barlow. a. Habit; b. inflorescence node with two triads (Womersley & Whitmore NGF 19070). Drawing by L. Spindler, reproduced from Blumea 41. Scale bars represent 1 cm.

Plant slender, erect, 50–80 cm in diam. *Stems* usually with rudimentary leaves on each growth segment; internodes terete or flattened upwards, (0–)10–25(–45) mm long, 0.5–2 mm in diam. *Leaves* usually rudimentary and normally developed in successive pairs; normally developed leaves linear to narrowly elliptic, attenuate to contracted at the base, more or less sessile, often undulate at the margin, rounded at the apex, obscurely 1-nerved, with veins usually not visible, (5–)10–40 by 1.5–4 mm; rudimentary leaves rarely lacking, rarely in two successive pairs, (0–)4–12 mm above each leafy node, 0.3–0.5 mm high. *Inflorescences* mostly terminal, mostly solitary, rarely in threes, rarely axillary, 1.5–10 mm long, a spike of 3–9(–16) pairs of single flowers or sometimes triads; internodes 0.5–1.5 mm long; the bracteal cup c. 0.3 mm long; bracteoles (when present) acute to truncate, almost entire or weakly serrate, c. 0.4 mm long. *Fruit* ellipsoid to almost globose, smooth, red.

Distribution — *Malesia*: Sumatra, Borneo.

Habitat & Ecology — Recorded in primary forests from 50 to 300 m altitude; recorded hosts include *Croton*, *Garcinia*.

Notes — 1. Rudimentary leaves sometimes quite basal, resembling true cataphylls.

2. When flowers are produced in triads the lateral flowers may develop later than the central one, which may be either male or female.

5. *Ginalloa nuda* Danser

Ginalloa nuda Danser, Rec. Trav. Bot. Néerl. 31 (1934) 229. — Type: *Clemens 31538*, Borneo, Sabah, Mt Kinabalu.

Plant slender, pendulous, 30–60 cm long. *Stems* with rudimentary leaves predominant on each growth segment; internodes terete, 15–60 mm long, 0.3–2 mm in diam. *Leaves* usually rudimentary, sometimes normally developed without regular pattern; normally developed leaves lanceolate, attenuate at the base to an obscure petiole 1–3 mm long, attenuate and finally shortly rounded at the apex, obscurely 3-nerved, 30–50 by 5–10 mm; rudimentary leaves 0.5–0.8 mm high. *Inflorescences* commonly axillary, sometimes terminal, solitary, 1.5–3 mm long, a spike of 2–3(–4) pairs of single flowers; internodes 0.6–1.2 mm long; bracteal cup c. 0.5 mm long, spreading. *Fruit* narrowly ellipsoid, smooth, red. — **Fig. 1 b, c.**

Distribution — *Malesia*: Borneo, recorded only from Mt Kinabalu.

Habitat & Ecology — 900–1350 m altitude; no hosts recorded.

Note — Similar to *Viscum* spp. in the predominantly leafless state and short inflorescence, but the anther structure and persistent tepals are characteristic of *Ginalloa*. Similar to *G. linearis*, differing in larger leaves and mostly shorter, predominantly axillary inflorescences.

6. *Ginalloa siamica* Craib

Ginalloa siamica Craib, Kew Bull. (1911) 455; Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 47. — Type: *Kerr 1300*, Thailand, Chiangmai.

Ginalloa siamica var. *scortechinii* Gamble, J. As. Soc. Beng. 75, ii (1914) 383; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 451. — Type: *Scortechini s. n.*, Perak.
Ginalloa ovata Danser, Philipp. J. Sc. 58 (1935) 133. — Type: *Oro FB 30844*, Luzon.

Plant moderately robust, erect, 50–80 cm in diam. *Stems* with rudimentary leaves on each growth segment; internodes terete or slightly dilated upwards, those bearing normally developed leaves 30–65 mm long, 1–5 mm in diameter. *Leaves* rudimentary and normally developed in successive pairs; normally developed leaves broadly elliptic to broadly ovate, cuneate at the base to an obscure petiole 2–4 mm long, rounded at the apex, 3- or 5-nerved, with veins visible on both sides, 25–60 by 20–40 mm; rudimentary leaves in pairs alternating regularly with normally developed leaves, 2–4 mm above each leafy node, ragged, c. 1 mm high. *Inflorescences* commonly terminal, often in threes, sometimes axillary, 20–35 mm long, a spike of 8–10 pairs of triads; internodes 1.5–5 mm long; bracteal cup c. 1 mm long, spreading; bracteoles acute, irregularly serrate, c. 0.5 mm long. *Fruit* ellipsoid, smooth or finely verrucose, not seen mature.

Distribution — Thailand, Cambodia; *Malesia*: Peninsular Malaysia, Philippines.

Habitat & Ecology — 400–1080 m altitude; the only recorded host is *Pentacme*.

KORTHALSELLA

Korthalsella Tiegh., Bull. Soc. Bot. France 43 (1896) 83, 163. — Type species: *Korthalsella remyana* Tiegh.

[For additional synonymy see Barlow, Brunonia 6 (1983) 37. The type species there cited for *Bifaria* should be *B. japonica* (Thunb.) Tiegh., not *B. rubra*].

Aerial stem-parasitic small perennials, entirely glabrous except for the floral cushions. *Stems* green or yellowish, usually articulated at the nodes; internodes terete or compressed or most often strongly flattened in one plane forming a cladode. *Leaves* opposite, rudimentary, each pair forming a border mostly less than 1 mm high at each node and subtending the flower clusters. *Flowers* developing successively in lateral clusters, usually surrounded and separated by multicellular sparsely branched thick-walled hairs (derived from floral bracts) which often form a raised mound (floral cushion); flower clusters sometimes coalescing and completely encircling the stem at each node; first-formed flower arising in an axillary position and usually male; subsequent flowers developing laterally to the first and often also in further transverse rows below the first, mostly female. *Male flowers* globose to obconic in bud, c. 0.5 mm in diam., attenuate at the base and shortly stipitate, 3-merous; tepals persistent, triangular, valvate; anthers 3, 2-locular, introrse, united into a synandrium with a common apical pore. *Female flowers* globose to pear-shaped, usually less than 0.5 mm in diam., 3-merous; tepals triangular; persistent at the top of the ovary. *Fruit* pear-shaped or ellipsoid, seldom reaching 3 mm in length, crowned by the persistent tepals. — **Fig. 3, 4.**

Distribution — 7–25 species (see below) distributed from Japan to Australia and New Zealand, extending eastwards to several Pacific archipelagos and westwards to Indian Ocean islands and Ethiopia. In *Malesia* 5 species, without a distinct centre of diversity.

The genus is exceptional among mistletoes for its range over remote islands, apparently the result of its atypical fruit structure and mode of dispersal (see under ecology, p. 404). The apparently fragmented distributions of some species may simply reflect their cryptic status in the field (see below).

Habitat & Ecology — Mostly in closed humid forests but extending to open woodlands and disturbed habitats (especially outside Malesia). In Malesia apparently most common in highlands above 1500 m but also known from lowland forests. The recorded occurrences may be to some extent an artifact of collecting because the minute plants may be rarely observed in the crowns of tall lowland rain forest trees, where they are usually found only when the host is sampled. The hosts are mostly dicotyledons, rarely conifers; for most species host specificity is low.

Morphology — *Korthalsella* is homogeneous in inflorescence and floral characters, but the species vary strikingly in general appearance owing to differences in vegetative characters and in the degree of differentiation of flower-bearing stems. In species with terete or weakly compressed internodes, the successive leaf pairs may be distichous or decussate. In species with strongly flattened internodes, the successive ones of each stem are always flattened in one plane. In some species virtually all nodes bear flower clusters, whereas in others flowering may be restricted to lateral stems or distal parts of stems. In such cases the flowering stems may be less flattened than the vegetative ones. The extreme of this development is illustrated by *K. geminata* (Fig. 3c,d), in which strongly flattened cladodes produce spike-like conflorescences in which the internodes are very short and terete. For additional illustrations of plant form in *Korthalsella* see Barlow, *Brunonia* 6 (1983) 40, 45, 50, 53.

The hairs which form the floral cushion are probably very densely fimbriate floral bracts, and therefore are homologous with the hairs in the inflorescences of some *Ginalloa* species (see there). In *K. geminata*, which lacks floral cushions, floral bracts are visible and are barely ciliate. Dissected floral bracts can also be seen in *K. japonica* and *K. papuana*.

Taxonomy — The most recently published revision of the entire genus is that of Danser, *Bull. Jard. Bot. Buitenzorg* III, 14 (1937) 115; 16 (1940) 329. The Australian species were revised by Barlow, *Brunonia* 6 (1983) 37. Danser recognized 23 species in the genus, and additions by Barlow only slightly outnumber reductions to synonymy, thus bringing the total to 25 species. Danser's and Barlow's treatments were based largely on external morphology, ecology and integrity of geographic occurrence. Touw, in *Blumea* 29 (1984) 525, reported a study of vascular structure in *Korthalsella*, and in subsequent unpublished work (Molvray 1990, see above) she used this as a major data set for a taxonomic revision. Although she accepted only 7 species in the genus, the nomenclatural implications for Malesia are minor, affecting only one species. However, Molvray's treatment of the entire genus has raised complex issues regarding species circumscription, and it has not been followed here.

For additional notes on taxonomic history, see Danser, *Bull. Jard. Bot. Buitenzorg* III, 14 (1937) 115 and Barlow, *Brunonia* 6 (1983) 37. Apart from the work of Danser the most significant earlier work was that of Van Tieghem in *Bull. Soc. Bot. France* 43

(1896) 83–87, 162–179. He was first to recognize *Korthalsella* as a genus distinct from *Viscum*, and subsequently distinguished two more genera, *Bifaria* and *Heterixia*, and more than 60 species. The latter genera are now regarded as congeneric with *Korthalsella*, and most of Van Tieghem's species names have been reduced to synonymy.

KEY TO THE SPECIES

- 1a. Flowers in terete spicate conflorescences which arise singly or in threes, terminally and laterally, these sharply distinct from the strongly flattened vegetative cladodes 2
- b. Flowers produced at nearly all nodes, or predominantly on more slender lateral cladodes, but not in strongly differentiated spicate conflorescences (the internodes of flowering branches showing a gradual rather than an abrupt transition in shape from the lower non-flowering ones) 3
- 2a. Flowers 3 in each cluster; conflorescences commonly lateral, sometimes terminal; conflorescence internodes 1–1.5 mm long **2. *K. geminata***
- b. Flowers 40 or more in each cluster; conflorescences rarely lateral, mostly terminal; conflorescence internodes 1.5–7 mm long **4. *K. papuana***
- 3a. Internodes terete, without visible veins; plants very slender, up to 3 cm long; hosts conifers **1. *K. dacrydii***
- b. Internodes compressed or flattened in one plane, with 1–3 veins visible as raised ribs; plants slender to robust, mostly more than 5 cm long; hosts dicotyledons . . . 4
- 4a. Largest internodes usually 1-ribbed, 5–12 mm long; plants mostly less than 10 cm long; flowers usually 8 or fewer in each cluster **3. *K. japonica***
- b. Largest internodes usually 3-ribbed, 10–27 mm long; plants mostly more than 10 cm long; flowers usually more than 10 in each cluster **5. *K. rubra***

1. *Korthalsella dacrydii* (Ridl.) Danser

Korthalsella dacrydii (Ridl.) Danser, Rec. Trav. Bot. Néerl. 31 (1934) 759; Bull. Jard. Bot. Buitenzorg III, 14 (1937) 124; Backer & Bakh. f., Fl. Java 2 (1965) 75. — *Arceuthobium dacrydii* Ridl., J. Fed. Malay States Mus. 6 (1916) 170; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 455. — Type: Ridley 16094, Malaya, Pahang, Mt Tahan.

Plants minute, to 3 cm long, slender, sparsely branched, not differentiated into distinct vegetative and flowering axes. *Stems* terete, to 10-noded; basal internode 2–3 mm long, 0.7–1 mm in diam.; succeeding internodes of the main stems to 9 mm long; distal flower-bearing internodes 1–3 mm long; venation not visible. *Rudimentary leaves* together encircling the node, c. 0.5 mm high, membranous, acute at the apices. Hairs of the *floral cushion* few, scarcely protruding, reddish. *Flowers* in 1 to 2 rows, 3–7 per cluster, the opposite clusters meeting and encircling the stem; male flowers solitary or with 2 subsidiary ones developing beside the first.

Distribution — *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java, Timor; recorded sporadically, possibly more widespread but overlooked owing to the very small size of the plants.

Habitat & Ecology — 950–1650 m altitude; apparently exclusively parasitic on conifers; recorded hosts are *Dacrydium* spp. and *Podocarpus imbricata* (*Dacrycarpus imbricatus*).

Note — Very similar to *K. salicornioides* of New Zealand and New Caledonia, differing in the prominent acute tips of the rudimentary leaves, and in its specificity for coniferous hosts. Differs from *K. grayi* of Australia in the same characters, together with the predominantly decussate phyllotaxy.

2. *Korthalsella geminata* (Korth.) Engl.

Korthalsella geminata (Korth.) Engl., Nat. Pflanzenfam., Nachtr. (1897) 138; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 453; 14 (1937) 129; 16 (1940) 331. — *Viscum geminatum* Korth., Verh. Bat. Genootsch. 17 (1839) 259. — *Heterixia geminata* Tiegh., Bull. Soc. Bot. France 43 (1896) 178. — Type: *Korthals s.n.*, Borneo, Mt Sakumbang.

Plants to 18 cm long, sparsely-branched vegetatively, differentiated into distinct vegetative and flowering axes. Stems with 8–12 vegetative internodes; basal internode usually terete or slightly angular, 2–3 mm long, 2–3 mm in diam.; succeeding internodes of the main stems progressively more strongly flattened, the largest ones narrowly to broadly elliptic or rarely almost linear, (10–)15–25 by (3–)6–15 mm; the vegetative branches mostly flattened in the same plane as the parent stem; venation with 3–7 veins distinct and raised and connecting veins usually visible. Rudimentary leaves together encircling the node, c. 0.5 mm high, leathery, acute at the apices. Flower-bearing stems forming terete spike-like confluences to 35 mm long, these usually solitary in the axils and sometimes terminal in threes; internodes 1–1.5 mm long; floral bracts c. 0.5 mm long, acute, sparsely and shortly ciliate. Hairs of the floral cushion absent. Flowers in 1 row, 3 per cluster; the male flower solitary and central. — **Fig. 3c, d.**

Distribution — *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Flores; recorded sporadically, possibly more widespread but overlooked owing to the small size of the plants.

Habitat & Ecology — Recorded from 1450 to 1740 m altitude; recorded hosts include *Garcinia*, *Rhodamnia* and *Syzygium*.

Note — Similar and probably related to *K. papuana*, differing in the characters set out in the key.

3. *Korthalsella japonica* (Thunb.) Engl.

Korthalsella japonica (Thunb.) Engl., Nat. Pflanzenfam., Nachtr. (1897) 138; Backer & Bakh. f., Fl. Java 2 (1965) 75. — *Viscum japonicum* Thunb., Trans. Linn. Soc. Lond. 2 (1794) 329. — Type: Herb. Thunberg.

Korthalsella brassiana Blakely, Proc. Roy. Soc. Queensland 47 (1936) 79. — *Korthalsella japonica* subsp. *brassiana* (Blakely) Barlow, Brunonia 6 (1983) 47. — Type: Brass 2298, Queensland, Thornton's Peak.

Viscum opuntia Thunb., Fl. Jap. (1784) 64, nom. superfl. — *Korthalsella opuntia* (Thunb.) Merr., Bot. Mag. Tokyo 30 (1916) 68, comb. illeg.; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 453; 14 (1937) 134; 16 (1940) 333; Philipp. J. Sc. 58 (1935) 134.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 14 (1937) 134, excluding *K. articulata* and names with epithets *breviarticulata*, *howensis* and *rubra*; Barlow, Brunonia 6 (1983) 48].

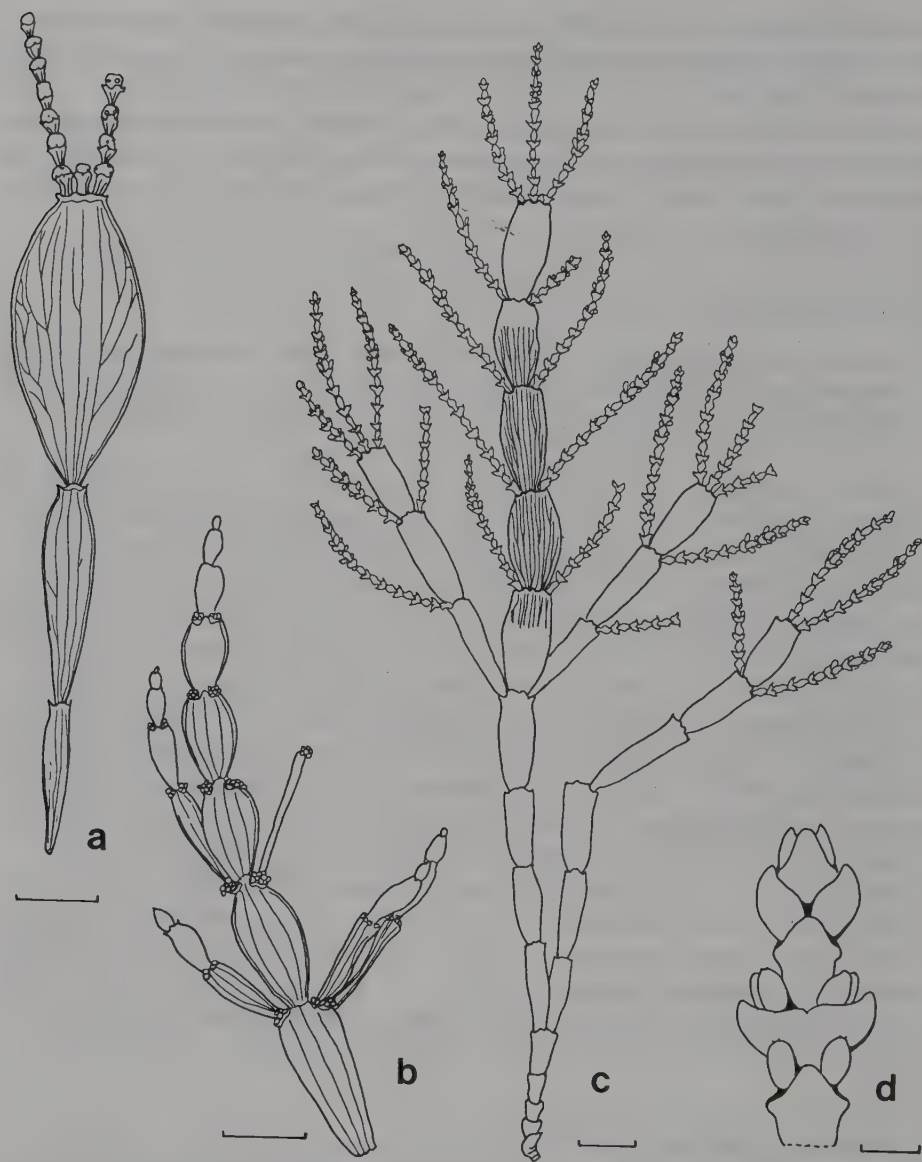


Fig. 3. *Korthalsella papuana* Danser. a. Habit. — *K. rubra* (Tiegh.) Engl. b. Habit. — *K. geminata* (Korth.) Engl. c. Habit; d. part of inflorescence (a: Hyland 8007; b: Hyland 6460; c, d: *Korthals* s.n.). Redrawn with permission from Flora of Australia 22 (a, b), and (c, d) from Danser (1937). Scale bars represent 1 cm (a, b, c), resp. 1 mm (d).

Plants 4–10(–20) cm long, relatively slender, much-branched, variable in appearance, sometimes with all branches similar to the main stems and sometimes with flowering branches distinctly narrower than the main vegetative ones although not strongly



Fig. 4. *Korthalsella japonica* (Thunb.) Engl. Photograph B. A. Barlow, 1982, macrophotograph from herbarium specimen. Reproduced with permission from Brunonia 6.

differentiated into abruptly distinct vegetative and flowering axes. *Stems* with 8–25 internodes; basal internode 2–12 mm long, terete and 1–2 mm in diameter when shorter, terete at the base and flattened up to 4 mm wide towards the apex when longer; succeeding internodes of the main stems flattened or compressed, narrowly cuneate to narrowly obovate, 5–12 by 2–4 mm; branches mostly flattened transversely to the plane of flattening of the parent stem; venation with 1 vein distinct and raised. *Rudimentary leaves* together encircling the node, 0.2–0.5 mm high, usually thin, truncate. Hairs of the *floral cushion* few or absent, developed from very small bracts, scarcely protruding, reddish. *Flowers* in 1 or 2 rows, c. 8 per cluster, the opposite clusters meeting and encircling the stem; male flowers usually solitary. — **Fig. 4.**

Distribution — Japan southwards to Australia, westwards to India and Indian Ocean islands, and possibly eastwards to Pacific islands; recorded sporadically, possibly more widespread and continuous but overlooked owing to the small size of the plants; in *Malaysia*: Sumatra, Peninsular Malaysia, Java, Philippines.

Habitat & Ecology — In Malesia recorded from mossy forest and ericoid brushwood from 1400 to 2700 m altitude; recorded hosts include *Diplycosia*, *Eurya*, *Rhododendron*, *Symplocos*, *Ternstroemia*, *Vaccinium*.

Notes — 1. For distinction as a species, see Barlow, *Brunonia* 6 (1983) 48.

2. In some specimens, especially from Sumatra, internodes of the flowering stems are short (1.5–2 mm long) and slightly compressed or almost terete, thus showing a gradation into spicate flowering axes, but not the abrupt transition present in *K. geminata* and *K. papuana*.

4. *Korthalsella papuana* Danser

Korthalsella papuana Danser, *Blumea* 3 (1938) 53; *Bull. Jard. Bot. Buitenzorg* III, 16 (1940) 331. — Type: *Carr 15120*, Papua, Main Range NW of The Gap.

Plants to 18 cm long, relatively unbranched vegetatively when young, branched at nearly every node when older, differentiated into distinct vegetative and flowering axes. *Stems* with 3–6 vegetative internodes; basal internode 2–3 mm long, terete and 1–2 mm in diameter, or up to 25 mm long and terete at the base and flattened up to 4 mm wide towards the apex; succeeding internodes of the main stems strongly flattened, the largest ones narrowly to broadly obovate, 16–55 by 10–22 mm; vegetative branches mostly flattened transversely to the plane of flattening of the parent stem; venation with 3–5 veins distinct and raised and connecting veins visible. *Rudimentary leaves* together encircling the node, c. 0.5 mm high, leathery, acute at the apices. *Flower-bearing stems* forming terete spike-like confluences 20–30(–50) mm long, these usually terminal in threes and sometimes solitary in the axils; the internodes 1.5–5(–7) mm long; floral bracts c. 0.3 mm long, coarsely dissected. Hairs of the *floral cushion* absent or few, coarse, scarcely protruding, red or black. *Flowers* in c. 4 rows, more than 40 per cluster, the opposite clusters meeting and encircling the stem in dense whorls; male flowers in the upper whorl. — **Fig. 3a.**

Distribution — Australia (Queensland); *Malesia*: New Guinea.

Habitat & Ecology — In Malesia from 2000 to 2900 m altitude; there recorded hosts include *Macaranga*, *Syzygium*, *Xanthomyrtus*.

Note — Similar and probably related to *K. geminata*, differing in the characters set out in the key.

5. *Korthalsella rubra* (Tiegh.) Engl.

Korthalsella rubra (Tiegh.) Engl., *Nat. Pflanzenfam.*, Nachtr. (1897) 138. — *Bifaria rubra* Tiegh., *Bull. Soc. Bot. France* 43 (1896) 173. — Type: *Mueller s.n.*, New South Wales, Richmond River. [For additional synonymy see Barlow, *Brunonia* 6 (1983) 51].

Plants 10–23 cm long, relatively robust, much-branched in the lower part with long unbranched extremities. *Stems* with 12–20 internodes; basal internode varying from terete, 5–12 mm long and 2–3 mm in diameter to flat, narrowly cuneate, to 18 mm long and 4 mm wide; succeeding internodes strongly flattened, narrowly cuneate to narrowly

obovate, 10–18(–27) by 3–10 mm; branches often with subsidiary ones arising from the same node, mostly flattened transversely to the plane of flattening of the parent stem; venation mostly with 3 veins distinct and raised. *Rudimentary leaves* together more or less encircling the node, 0.2–1 mm high, leathery, truncate. Hairs of the *floral cushion* sparse to dense, usually protruding, usually red or white. *Flowers* in 2–5 rows, 10–80 per cluster, the opposite clusters not meeting to encircle the stem; male flowers few in all rows. — **Fig. 3b.**

Distribution — Eastern Australia, Lord Howe I.; *Malesia*: New Guinea (New Ireland, Lousiade Archipelago); possibly more widespread in New Guinea but overlooked owing to the small size of the plants.

Habitat & Ecology — Closed and open forests; in *Malesia* in humid forests at 0–1000 m altitude; there recorded hosts include *Aceratium*, *Planchonella*, *Platea* and *Rhodamnia*.

Note — For distinction as a species see Barlow, *Brunonia* 6 (1983) 52. In unpublished work, Molvray (1990) has proposed the inclusion of *K. rubra* in a more broadly circumscribed species under the name *K. taenioides*.

NOTOTHIXOS

Notothixos Oliv., J. Linn. Soc. Bot. 7 (1864) 92, 103. — Type species: *Notothixos subaureus* Oliv., lecto.

[For additional synonymy see Barlow, *Brunonia* 6 (1983) 2].

Aerial stem-parasitic shrubs, densely velvety tomentose on young parts. *Stems* much-branched; branches with a pair of prophylls at the base of the first internode and a decussate pair of rudimentary leaves (cataphylls) just above the base. *Leaves* opposite, petiolate, entire, bifacial, curvinerved, usually with 3 or 5 veins visible on the upper surface. *Inflorescences* terminal, of 1 or more fan-shaped cymules, these solitary or in a racemose or spicate arrangement; cymules with 3–13 flowers developing successively from the centre outwards, with the central flowers male and the lateral flowers female; bracts small, triangular, in pairs subtending each cymule. *Male flowers* globose, c. 1 mm in diam., shortly stipitate, usually 4-merous; tepals triangular, valvate; anthers depressed-ovoid or reniform, many-loculate, opening by pores, on a short filament. *Female flowers* cylindric or barrel-shaped, usually less than 2 mm long, 4-merous; tepals triangular; stigma small, nipple-shaped. *Fruit* narrowly ellipsoid to almost globose, crowned by the persistent tepals. — **Fig. 5–8.**

Distribution — Eight species distributed from Sri Lanka eastwards and southwards to eastern Australia and the Santa Cruz Islands. In *Malesia* 6 species, with a centre of diversity in New Guinea.

Habitat & Ecology — Mostly in closed humid forests but extending to open woodlands and disturbed habitats, common in lowlands but extending to 2000 m altitude in New Guinea. For most species host specificity is low.

Morphology — All species of *Notothixos* have a dense, copious indumentum on the young parts, usually persisting at least on the leaf undersides, inflorescences and flow-

ers. This easily distinguishes the genus from *Viscum*, in which all species are glabrous. The tomentum is creamy white to brown, often golden, and comprises mixed unicellular and multicellular hairs. The unicellular hairs are stellate, sometimes dilated into peltate scales. The multicellular hairs are dendritic, consisting of several to many stellate cells in series. For discussion and illustration see Barlow, *Brunonia* 6 (1983) 5.

The basic inflorescence unit is a small cymose cluster subtended by a pair of small bracts. It becomes fan-like as successive flowers develop laterally. In some species the inflorescence is a single terminal cymule, but in others it is expanded in racemose or spicate fashion, usually with decussate pairs of cymules. In some cases these complex inflorescences are determinate, producing a terminal cymule, and in other cases are indeterminate. For discussion and illustration see Barlow, *Brunonia* 6 (1983) 6.

Taxonomy — For a revision of the genus and discussion of relationships and biogeography, see Barlow, *Brunonia* 6 (1983) 1.

KEY TO THE SPECIES

- 1a. Inflorescence a single terminal cymule; indumentum consisting of peltate scales mixed with dendritic hairs **4. *N. malayanus***
- b. Inflorescence of 3 or more cymules on a common axis; indumentum lacking peltate scales among the dendritic and stellate hairs 2
- 2a. Inflorescence of 3 or 4 decussate cymules, each produced from the central bud of the one below it **5. *N. papuanus***
- b. Inflorescence of 3 to many cymules on a common axis, borne laterally in 1 or more decussate pairs, with or without a terminal cymule 3
- 3a. Lateral cymules pedunculate, each with 5–11 flowers 4
- b. Lateral cymules sessile, each 3-flowered 5
- 4a. Tomentum cream to brown, mostly golden, persisting as a dense felt on the lower leaf surfaces; cataphylls narrowly triangular, not sheathing the stem, not at a visible nodal articulation **3. *N. leiophyllus***
- b. Tomentum white or tawny, becoming sparse on lower leaf surfaces with age; cataphylls broadly triangular, partly sheathing the stem, often at a nodal articulation **1. *N. cornifolius***
- 5a. Young leaves with tomentum similar on both sides; leaf lamina 12–15(–20) mm wide; inflorescence axis 15–20(–40) mm long with 7–10 pairs of triads **2. *N. floccosus***
- b. Young leaves usually with tomentum paler on the upper side; leaf lamina (5–)22–30(–50) mm wide; inflorescence axis 30–60 mm long with 9–14 pairs of triads **6. *N. sulphureus***

1. *Notothixos cornifolius* Oliv.

Notothixos cornifolius Oliv., J. Linn. Soc. Bot. 7 (1864) 103; Barlow, *Brunonia* 6 (1983) 18. — Type: *Cunningham* 50, New South Wales, Liverpool Plains.
[For additional synonymy see Barlow, l.c.]

Indumentum short, white or tawny, sparse on mature parts with only scattered hairs remaining. *Stem* prophylls c. 0.3 mm long, broadly acute; cataphylls c. 1 mm long, acute, partly sheathing the stem. *Leaf* lamina narrowly elliptic or ovate, (3.5–)4.5–7(–9) by (1–)1.5–2.5(–4) cm, sometimes falcate, attenuate at the base to a petiole 5–10 mm long, somewhat attenuate and rounded to acute at the apex. *Inflorescence* an indeterminate raceme of 4–11 decussate pairs of cymules, often with subsidiary racemes at the base; axis 25–60(–90) mm long; peduncles of the cymules 2–5 mm long; cymules 5- to 11-flowered with the central 1–5 flowers male. — **Fig. 5b, c.**

Distribution — Eastern Australia; *Malesia*: eastern New Guinea.

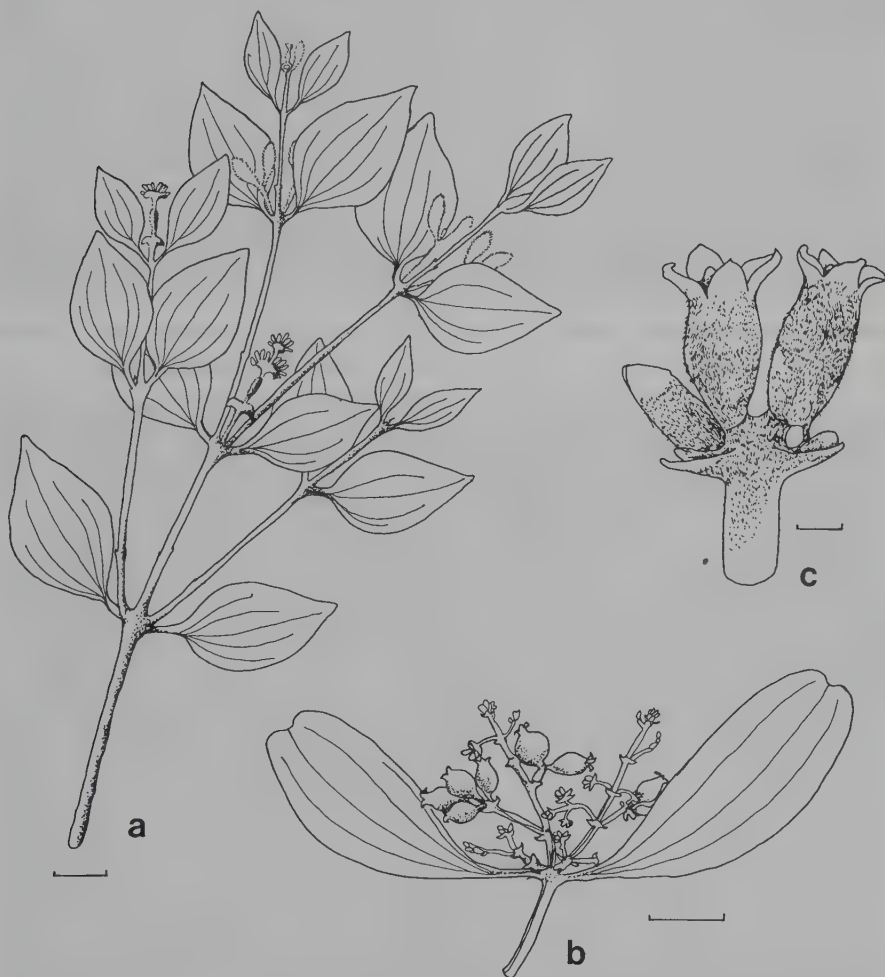


Fig. 5. *Nothothixos papuanus* Danser. a. Habit. — *Nothothixos cornifolius* Oliv. b. Branchlet with flowers and fruits; c. cymule from inflorescence (a: Carr 15403; b, c: Barlow 3742). Redrawn with permission from Flora of Australia 22 (b, c), and (a) from Danser (1938). Scale bars represent 1 cm (a, b), resp. 1 mm (c).

Habitat & Ecology — 0–1680 m altitude; other habitat details not known for Malesia; in Australia in open and closed forests, almost exclusively parasitic on *Sterculiaceae* (*Argyrodendron*, *Brachychiton*, *Sterculia*); also recorded on *Jagera*.

Note — Common in eastern Australia but known from only a single collection in New Guinea.

2. *Notothixos floccosus* (Thwaites) Oliv.

Notothixos floccosus (Thwaites) Oliv. ex Hook. f., Fl. Brit. India 5 (1885) 227; Barlow, Brunonia 6 (1983) 19. — *Viscum floccosum* Thwaites, Enum. Pl. Zeyl. (1864) 418. — Type: *Thwaites CP 3654*, Sri Lanka, between Ambalangoda and Ratnapura.

Notothixos curranii Merr., Philipp. J. Sc., Bot. 4 (1909) 152; Danser, Philipp. J. Sc. 58 (1935) 136. — Type: *Merritt & Curran FB 12402*, Luzon, Mt Limay.

Notothixos spicatus K. Krause, Bot. Jahrb. 57 (1922) 465, 492; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 458; Backer & Bakh. f., Fl. Java 2 (1965) 75. — Type: *Ledermann 9841*, New Guinea, 'Etappenberg'.

Notothixos merguiensis Danser, Blumea 3 (1940) 392. — Type: *Braybon's Collector 201*, Burma, Leikok Chuang.

Indumentum dense, cream to greenish gold or light pinkish brown, becoming dull with age and soon disappearing from vegetative parts. *Stem* prophylls and cataphylls narrow, acute, up to 0.5 mm long, appressed, apparently deciduous. *Leaf* lamina ovate to broadly ovate or broadly elliptic, 1.5–3(–4) by 1.2–1.5(–2) cm, attenuate or cuneate at the base to a petiole c. 5 mm long, shortly attenuate and rounded or rarely acute or obtuse at the apex. *Inflorescence* an indeterminate spike of 7–10 decussate pairs of cymules; axis 15–20(–40) mm long, with tufts of hairs prominent at the nodes; cymules 3-flowered with the central flower male and a bract under each flower.

Distribution — Sri Lanka, Burma; in *Malesia*: from Philippines, Borneo and Java to New Guinea.

Habitat & Ecology — 0–1600 m altitude; recorded hosts include *Elaeocarpus* and *Gironniera*.

Notes — 1. Closely related to *N. sulphureus*; for differences see Barlow, Brunonia 6 (1983) 22.

2. For distinction as a species and conspecificity of *N. curranii*, *N. merguiensis* and *N. spicatus*, see Barlow, l.c.: 20.

3. *Notothixos leiophyllus* K. Schum.

Notothixos leiophyllus K. Schum. in K. Schum. & Lauterb., Fl. Deutsch. Schutzgeb. Südsee, Nachtr. (1905) 260; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 456; Philipp. J. Sc. 58 (1935) 130; Barlow, Brunonia 6 (1983) 15. — Type: *Parkinson 105*, New Britain.

Notothixos philippense Elmer, Leaf. Philipp. Bot. 2 (1908) 47. — Type: *Elmer 10114*, Negros Or., Cuernos Mts.

Notothixos schlechteri K. Krause, Bot. Jahrb. 57 (1922) 465, 493; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 458. — Type: *Schlechter 17662*, New Guinea, Kani Mts.

Notothixos ledermannii K. Krause, Bot. Jahrb. 57 (1922) 465, 494. — Type: *Ledermann 6975*, New Guinea, near Malu.

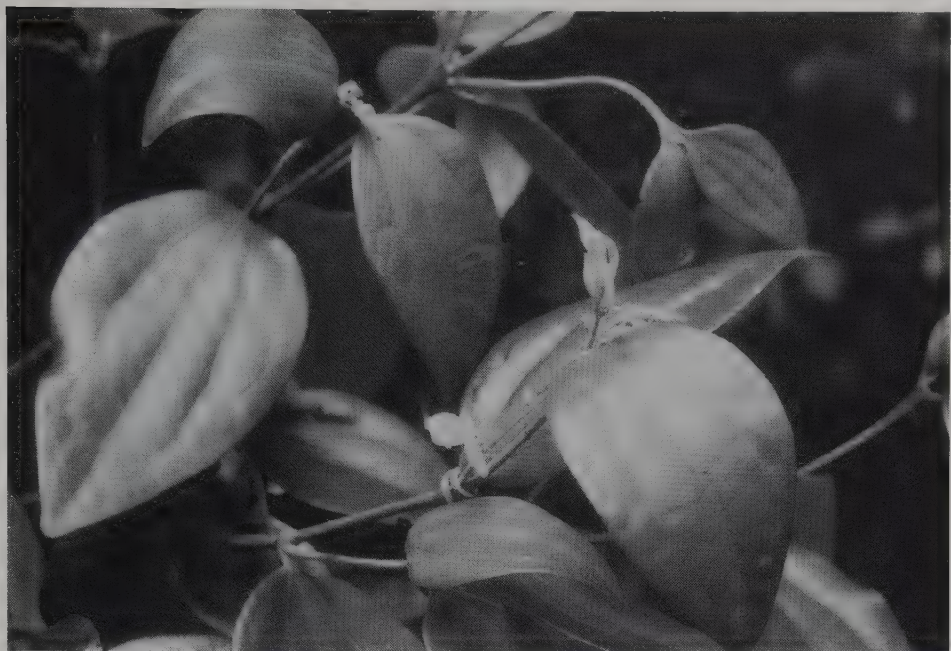


Fig. 6. *Notothixos leiophyllus* K. Schum. Leafy branches with one young inflorescence. Queensland, Kuranda. Photograph W.N.B. Quick, 1982, with permission.



Fig. 7. *Notothixos leiophyllus* K. Schum. Inflorescence, detail, with immature fruits. Queensland, Cardwell. Photograph M.F. Braby, 1991, with permission.

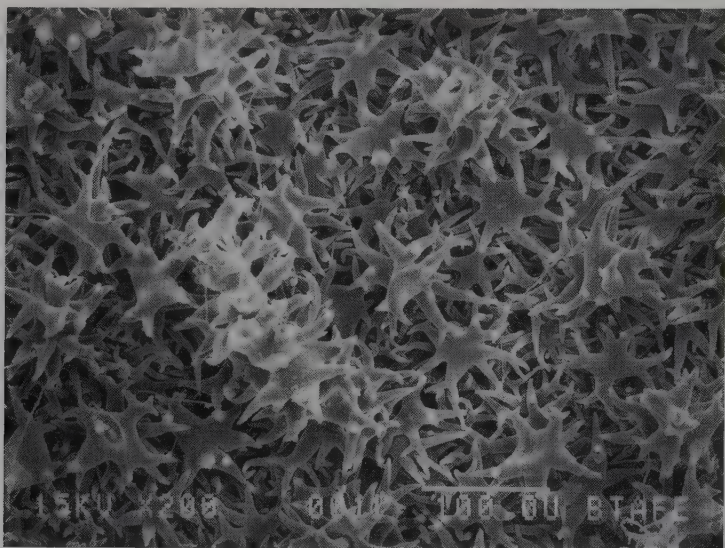


Fig. 8. *Nothothixos leiophyllus* K. Schum. Scanning electron micrograph of lower leaf surface, showing dendritic and stellate hairs. Reproduced with permission from Brunonia 6.

Indumentum short, creamy to golden or rarely rusty, becoming dull with age and soon disappearing from stems and leaf upper surfaces. *Stem* prophylls and cataphylls narrow, acute, c. 1 mm long, the cataphylls often unequally accrete 1–4 mm above the base of the internode. *Leaf* lamina narrowly to broadly elliptic or ovate, (4–)5–10(–15) by 2–4(–7) cm, cuneate to truncate at the base to a petiole 5–10 mm long, acuminate and rounded at the apex with a short blunt mucro. *Inflorescence* an indeterminate raceme of 6–12 decussate pairs of cymules, often with subsidiary cymules developing below them in the axils of the same bracts, rarely determinate with a terminal cymule; axis up to 10 cm long; peduncles of the cymules 2–5 mm long; cymules 5- to 9-flowered with the central 0–3 flowers male. — **Fig. 6–8.**

Distribution — Northeastern Queensland, Solomon Islands, Santa Cruz; in *Malesia*: from Philippines southwards to Flores and eastwards to New Guinea.

Habitat & Ecology — Primary and secondary humid forests and cultivated lands, from 0 to 1200 m altitude; recorded hosts include *Aegle*, *Citrus*, *Decaisnina*, *Dendrophthoe*, *Elaeocarpus*, *Gironniera*, *Haplolobus*, *Macaranga*, *Pangium*, *Pometia*, *Prunus*.

Note — For distinction as a species, differences from *N. cornifolius* and conspecificity of *N. ledermannii*, *N. philippinense* and *N. schlechteri*, see Barlow, Blumea 6 (1983) 16.

4. *Nothothixos malayanus* Oliv.

Nothothixos malayanus Oliv. in Hook., Ic. Pl. 16 (1886) t. 1519; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 457; Barlow, Brunonia 6 (1983) 10. — Type: Curtis 233, Penang.

Indumentum dense, of peltate, stipitate, disc-shaped unicellular scales each with 4–8 scattered tooth-like processes, mixed with scattered dendritic hairs, disappearing with age from stems and leaf upper surfaces. *Stem* prophylls and cataphylls narrow, acute, c. 0.7 mm long. *Leaf* lamina elliptic to broadly elliptic, 2.5–4 by 2–3 cm, attenuate or cuneate at the base to a petiole 3–5 mm long, rounded at the apex. *Inflorescence* a single pedunculate cymule of c. 7 flowers with the central 1–3 flowers male; peduncle c. 2 mm long, elongating to c. 6 mm long in fruit.

Distribution — *Malesia*: Peninsular Malaysia (Penang I.).

Habitat & Ecology — 0–210 m altitude; no hosts recorded.

Note — Apparently not collected since 1910; assessment of the conservation status of the species is desirable.

5. *Notothixos papuanus* Danser

Notothixos papuanus Danser, *Blumea* 3 (1938) 56; Barlow, *Brunonia* 6 (1983) 13. — Type: *Carr 13660*, Papua, Alola.

Indumentum dense, golden, becoming sparse on leaf upper surfaces. *Stem* prophylls and cataphylls narrow, acute, 0.5–1 mm long, almost obscured by the indumentum, with the cataphylls accrete up to halfway along the basal internode. *Leaf* lamina ovate to broadly ovate, 2.5–4 by 1.5–3 cm, cuneate at the base to a petiole 3–5 mm long, acute and sometimes shortly acuminate at the apex. *Inflorescence* spike-like, actually a determinate series of 3 to 4 decussate pedunculate cymules, each produced from the central bud of the one below it; axis with a basal internode 8–10 mm long and succeeding internodes 4–8 mm long; cymules up to 12-flowered with the central 2–6 flowers male. —

Fig. 5a.

Distribution — *Malesia*: New Guinea.

Habitat & Ecology — Closed humid forests from 1200 to 2100 m altitude; recorded hosts include *Palaquium* and *Planchonella*.

Note — For discussion of inflorescence structure see Barlow, l.c.

6. *Notothixos sulphureus* Merr.

Notothixos sulphureus Merr., *Philipp. J. Sc., Bot.* 4 (1909) 152; Danser, *Philipp. J. Sc.* 58 (1935) 137; Barlow, *Brunonia* 6 (1983) 22. — Type: *Whitford & Hutchinson FB 9132*, Mindanao, Zamboanga.

Indumentum long and dense, cream to golden or rusty, mostly paler on young leaf upper surfaces, soon disappearing from the stems and leaf upper surfaces. *Stem* prophylls and cataphylls narrow, acute, c. 1 mm long, the cataphylls often unequally accrete (2–)4–7(–40) mm above the base of the internode. *Leaf* lamina ovate to broadly ovate, (2–)2.5–4(–6) by (1.5–)2–3(–5) cm, cuneate to slightly cordate at the base to a petiole (1–)3–5(–7) mm long, rounded but sometimes shortly attenuate at the apex. *Inflorescence* an indeterminate spike of 9–14 decussate pairs of cymules; axis 3–6 cm long, with dense tufts of hairs prominent at the nodes; cymules 3-flowered with the central flower usually male and a bract under each flower.

Distribution — *Malesia*: Borneo, Philippines (Mindanao), Celebes.

Habitat & Ecology — 0–1220 m altitude; no hosts recorded.

Note — Closely related to *N. floccosus*; for differences see Barlow, l.c.

VISCUM

Viscum L., Sp. Pl. 2 (1753) 1023; Gen. Pl., ed. 5 (1754) 448. — Type species: *Viscum album* L. *Aspidixia* (Korth.) Tiegh., Bull. Soc. Bot. France 43 (1896) 191. — *Viscum* sect. *Aspidixia* Korth., Verh. Bat. Genootsch. 17 (1839) 235. — Type species: *Viscum articulatum* Burm. f.

Aerial stem-parasitic shrubs, glabrous, monoecious or (not in *Malesia*) dioecious. *Stems* much-branched; internodes terete or compressed or flattened decussately, often longitudinally ridged or striate. *Leaves* opposite, normally developed or rudimentary; normally developed leaves entire, unifacial, curvinerved, usually with 3 or 5 veins visible; rudimentary leaves bract-like, c. 1 mm long. *Inflorescences* terminal or axillary, basically a 3-flowered cymule, sometimes reduced to 1 flower or enlarged by development of adventitious flowers; bracts small, triangular, in pairs forming a boat-shaped cupule subtending each cymule. *Male flowers* flattened, 0.5–1.5 mm long, 4-merous; tepals triangular, valvate; anthers disc-shaped, many-loculate, opening by pores, sessile and fused to the tepal. *Female flowers* cylindric, at anthesis usually less than 2 mm long, 4-merous; tepals triangular; stigma small, nipple-shaped. *Fruit* narrow-ellipsoid to globose, smooth or tuberculate; tepals usually caducous, rarely persistent as a crown on the fruit. — **Fig. 9–13.**

Distribution — Genus of c. 100 species distributed in Europe, throughout Africa, and eastwards to eastern Asia, *Malesia* and Australia. In *Malesia* 9 species, of which probably 4 are endemic, without a distinct centre of species richness.

Habitat & Ecology — Occurs in a range of habitats from closed humid forests to open woodlands and disturbed habitats; in *Malesia* usually in lowlands to 1500 m but reaching 2300 m in Java. For most species host specificity is low, but some species occur commonly or exclusively on other mistletoes of the families *Loranthaceae* and *Viscaceae*.

Morphology — In most species of *Viscum* the stems long remain green. The basic inflorescence unit is a small 3-flowered dichasium (cymule), in *Malesia* usually with both male and female flowers, although all-female cymules are sometimes produced when flowering is prolific. In some monoecious species the male flowers are central in the cymule; in others they are lateral. Cymules often develop successively at each node.

Biogeography — The greatest diversity in *Viscum* occurs in Africa and southern Asia. Dioecy is a derived state which has probably arisen in Africa and spread to Europe and temperate Asia, but has not reached *Malesia*. The *Malesian* species probably represent an earlier phase of expansion of the monoecious stocks from a Laurasian source, with a gradual attenuation of species richness southeastwards to Australia. For discussion see Barlow in Calder & Bernhardt (eds.), *The Biology of Mistletoes* (1983) 19–46; in Baas et al. (eds.), *The Plant Diversity of Malesia* (1990) 273–292.

Taxonomy — For a revision of Asian and *Malesian* species, see Danser, *Blumea* 4 (1941) 261–319.

KEY TO THE SPECIES

- 1a. Plants seemingly leafless. 2
- b. Plants leafy 6
- 2a. Inflorescence with a peduncle 2–4 mm long; fruit tuberculate **2. V. exile**
- b. Inflorescence sessile or nearly so; fruit smooth or papillose 3
- 3a. Fruit papillose, with persistent tepals at the apex **4. V. loranthi**
- b. Fruit smooth, without persistent tepals at the apex 4
- 4a. Stem internodes quite flat, 3–10 mm wide **5. V. nepalense**
- b. Stem internodes terete or if flattened distinctly angular, 0.5–3(–5) mm wide 5
- 5a. Fruit globose, white; internodes angular **1. V. articulatum**
- b. Fruit ellipsoid, yellow; internodes terete or angular, distinctly longitudinally ribbed **8. V. stenocarpum**
- 6a. Fruit tuberculate 7
- b. Fruit smooth or minutely punctate. 8
- 7a. Leaves linear, less than 3 mm wide, soon falling **2. V. exile**
- b. Leaves narrowly elliptic to obovate, 10–35 mm wide, long persistent **6. V. ovalifolium**
- 8a. Male flowers, when present, central in the inflorescence **3. V. katikianum**
- b. Male flowers, when present, lateral in the inflorescence 9
- 9a. Leaves linear, 3–5 mm wide **7. V. scurruloideum**
- b. Leaves spatulate to obovate, 12–25 mm wide **9. V. wrayi**

1. *Viscum articulatum* Burm. f.

Viscum articulatum Burm. f., Fl. Indica (1768) 211; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 460; 16 (1938) 56; Philipp. J. Sc. 58 (1935) 141; Blumea 4 (1941) 280; Backer & Bakh. f., Fl. Java 2 (1965) 76. — Type: *Pryon s.n.*, Java.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 460; 16 (1938) 48; Philipp. J. Sc. 58 (1935) 141; Blumea 4 (1941) 280].

Plant slender, pendulous. *Stem* internodes at maturity decussately flattened or compressed, quadrangular or double-edged with a raised angular rib on each face, 15–50 mm long, 0.5–3 mm wide below, widened to 1–5 mm above. *Leaves* rudimentary, spreading, c. 0.5 mm long. *Inflorescence* axillary, a sessile cymule of 1 flower subtended by a cupule c. 1 mm long, with subsidiary cymules developing lateral to the first one, with the first-formed flower female and the lateral flowers female or male. *Fruit* globose, sessile, smooth, white. — **Fig. 9a, 10.**

Distribution — Eastern India eastwards to Vietnam and southwards to eastern Australia; *Malesia*: widespread throughout the region.

Habitat & Ecology — Open and closed forests from 0 to 1500 m altitude; usually parasitic on *Loranthaceae* and other *Viscaceae*; many recorded tree hosts may be in error, overlooking the secondary parasitism.

Note — Very similar vegetatively to *V. stenocarpum*; for differences see there. Also closely related to and possibly intergrading with *V. nepalense*; for distinction see there.

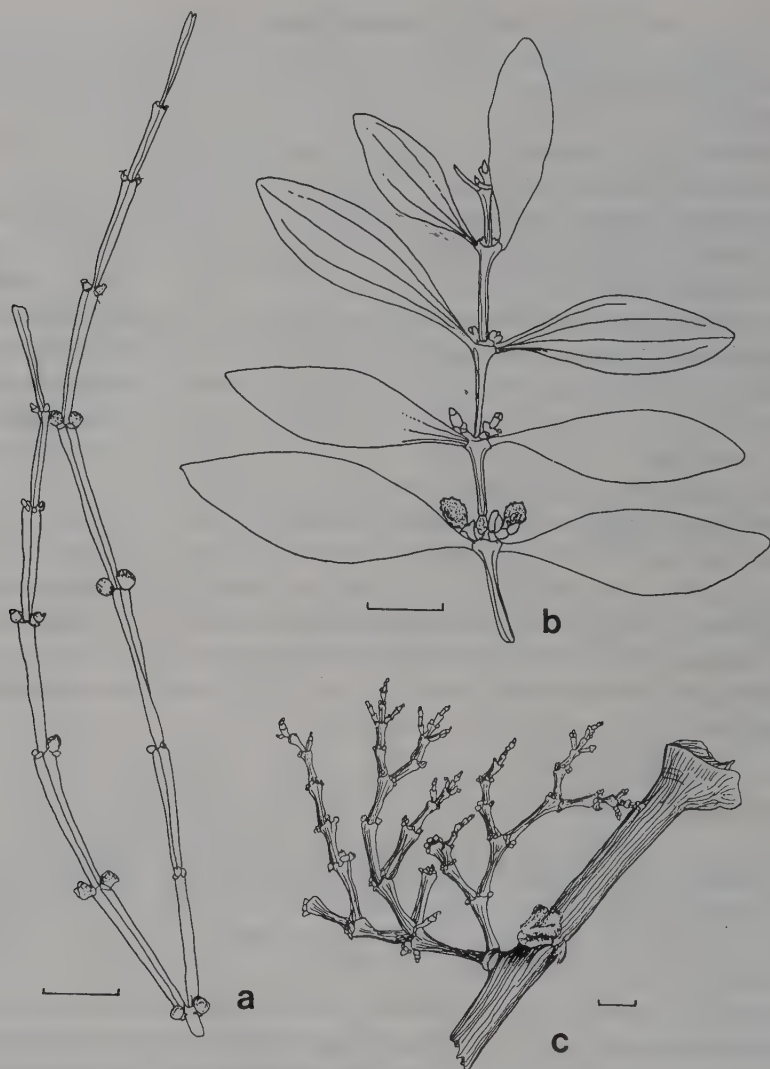


Fig. 9. *Viscum articulatum* Burm. f. a. Habit. — *V. ovalifolium* DC. b. Habit. — *V. loranthe* Elmer. c. Habit (a: Dockrill 847; b: Barlow 3718; c: Jacobson 2162). Redrawn with permission from Flora of Australia 22 (a, b), and (c) from Danser (1931). Scale bars represent 1 cm.

2. *Viscum exile* Barlow

Viscum exile Barlow, Blumea 41 (1996) 343. — Type: *Eyma 3721*, Celebes, Poso.

Plant slender, pendulous. *Stem* internodes terete, longitudinally ridged, 25–80 mm long, 0.5–1 mm in diam. *Leaves* normally developed or rudimentary, the normal ones probably caducous; lamina in normal leaves flat, linear, attenuate at the base to an obscure petiole 1–2 mm long, attenuate and acute at the apex, 35–50 mm long, 1–2 mm



Fig. 10. *Viscum articulatum* Burm. f. Ripe fruits. Queensland, Townsville. Photograph M.F. Braby, 1992, with permission.

wide in the middle, without visible venation; rudimentary leaves occasional, spreading, narrow, acute, c. 1 mm long. *Inflorescence* axillary, a pedunculate cymule of 3 flowers subtended by a cupule c. 0.5 mm long, with the middle flower female and the lateral flowers male; peduncle 2–4 mm long. *Fruit* globose, contracted at the base to a stipe c. 0.5 mm long, tuberculate, green. — **Fig. 11a–c.**

Distribution — *Malesia*: Celebes.

Habitat & Ecology — Not known.

Note — Similar to some forms of *V. ovalifolium* in inflorescence characters, but sharply distinct vegetatively. Superficially the plant appears leafless because of the very narrow leaves which fall early.

3. *Viscum katikianum* Barlow

Viscum katikianum Barlow, Trans. Roy. Soc. S. Austral. 95 (1971) 53. — Type: Barlow 947, Papua New Guinea, Wau.

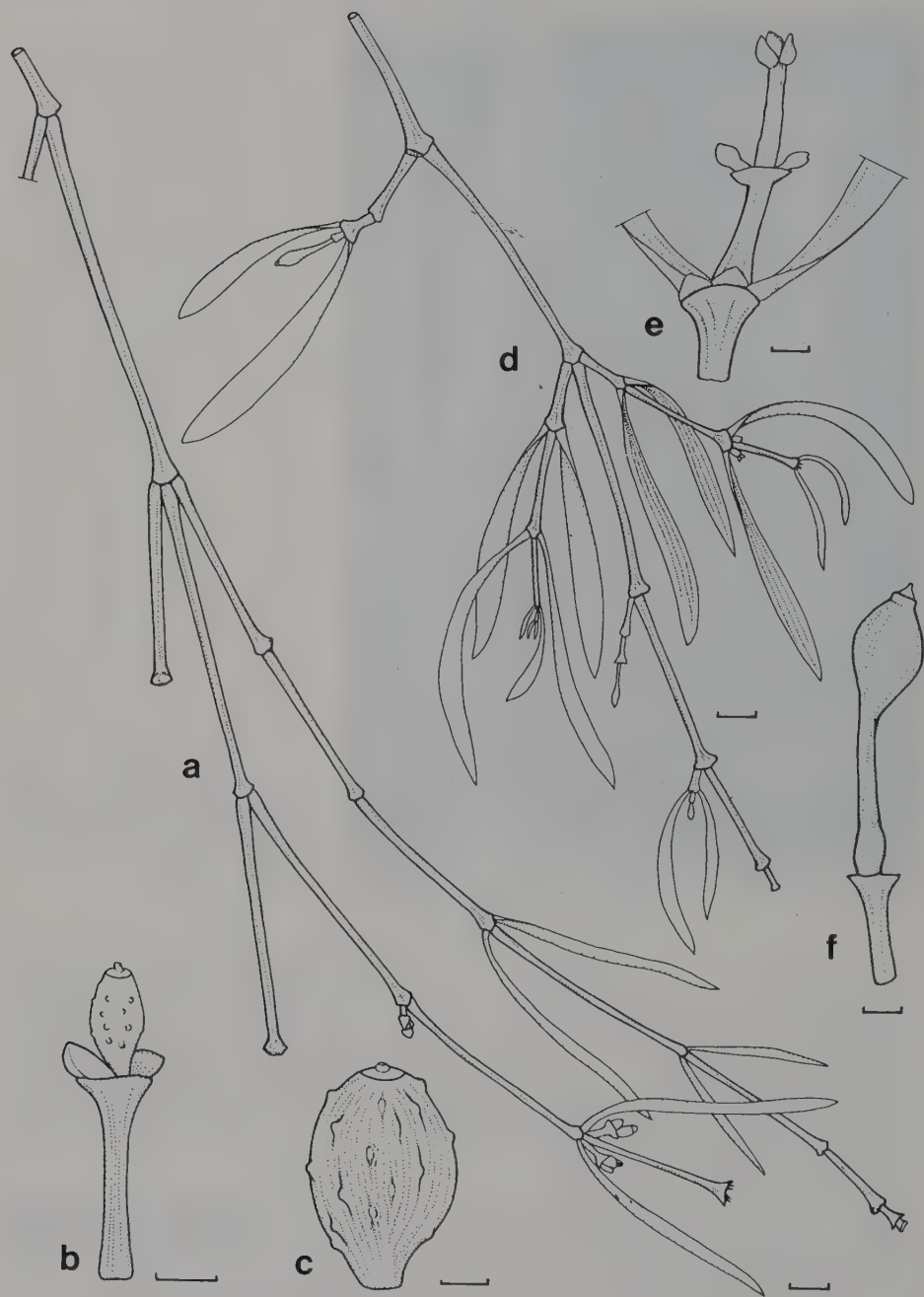


Fig. 11. *Viscum exile* Barlow. a. Habit; b. inflorescence with young fruit; c. immature fruit. — *V. scurruloideum* Barlow. d. Habit; e. inflorescence; f. fruiting inflorescence (a – c: *Eyma* 3721; d–f: *Hildebrand* s. n.). Drawing by L. Spindler, reproduced from *Blumea* 41. Scale bars represent 1 cm (a, d), resp. 1 mm (b, c, e, f).

Plant slender, erect. *Stem* internodes terete, slightly flattened upwards, striate, 25–60 mm long, 2–3 mm diameter below, widened to 2.5–4 mm above. *Leaves* mostly normally developed; lamina lanceolate to ovate, often falcate, attenuate at the base to an obscure petiole 5–10 mm long, obtuse to acute and sometimes mucronate at the apex, 3- or 5-nerved, 60–100 by 13–45 mm. *Inflorescence* axillary, a pedunculate cymule of 3 flowers subtended by a cupule 1–2 mm long, with subsidiary cymules developing adjacent to the first, with the middle flower male or female and the lateral flowers female; peduncle 4–6 mm long, elongating slightly in fruit. *Fruit* ellipsoid, shortly stipitate, finely punctate.

Distribution — *Malesia*: Papua New Guinea.

Habitat & Ecology — 400–1400 m altitude; recorded hosts include *Alyxia* and *Amyema*.

Note — Probably related to *V. whitei* of northern Australia, from which it differs in its more rigid stems, more erect growth and much larger leaves.

4. *Viscum loranthei* Elmer

Viscum loranthei Elmer, Leafl. Philipp. Bot. 8 (1919) 3089; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 464; Philipp. J. Sc. 58 (1935) 142; Blumea 4 (1941) 295. — Type: *Elmer 17777*, Luzon, Mt Maquililing.

Plant moderately robust, erect, 10–25 cm tall. *Stem* internodes terete, longitudinally ridged, 5–20 mm long, 1–3 mm wide, enlarged at the nodes. *Leaves* rudimentary, each opposite pair forming a spreading collar c. 0.5 mm wide. *Inflorescence* axillary, a sessile cymule of 1–3 flowers subtended by a cupule c. 0.5 mm long, with many subsidiary cymules of 1–3 flowers soon developing adjacent to the first one, with the middle flower female and the lateral flowers (when present) male or female. *Fruit* urceolate, sessile, coarsely wrinkled when dry, crowned by the persistent tepals. — **Fig. 9c.**

Distribution — Himalayas eastwards to southern China; *Malesia*: Sumatra, Philippines.

Habitat & Ecology — In uplands, mostly 900–1800 m altitude, rarely to 2650 m; recorded hosts are three closely related genera of *Loranthaceae* (*Dendrophthoe*, *Scurrula*, *Taxillus*).

Note — Distinctive in the genus in having the tepals persistent on the fruit. This character otherwise distinguishes *Viscum* from all other genera of *Viscaceae* in *Malesia*.

5. *Viscum nepalense* Spreng.

Viscum nepalense Spreng., Syst. Veg., Cur. post. (1827) 47; Danser, Blumea 4 (1941) 283. — Types: *Hamilton s.n.*; *Wallich s.n.*, Nepal.

Viscum dichotomum auct. non Gilibert (1792): D. Don, Prod. Fl. Nepal. (1825) 142.

Viscum articulatum auct. non Burm. f.: Backer & Bakh. f., Fl. Java 2 (1965) 76, p.p.

[For additional synonymy see Danser, Blumea 4 (1941) 283].

Plant slender to robust, pendulous. *Stem* internodes flattened, widest above the middle or at the apex, with 1–5 longitudinal veins raised and distinct on each side and the

middle one often more prominent, 20–60 mm long, 3–10 mm wide. *Leaves* rudimentary, erect, 0.2–0.3 mm long. *Inflorescence* axillary, a sessile cymule of 1 flower subtended by a cupule c. 1 mm long, with subsidiary cymules developing lateral to the first one, with the first-formed flower female and the lateral flowers female or male. *Fruit* globose or slightly ellipsoid, sessile, smooth, pale coloured, probably yellowish. — **Fig. 12.**



Fig. 12. *Viscum* prob. *nepalense* Spreng. Habit. Kalimantan, Sanggau. Photograph A. Elsener, 1961.

Distribution — From India eastwards to southern China; *Malesia*: Sumatra, Peninsular Malaysia, Borneo, Java.

Habitat & Ecology — 50–1600 m altitude; recorded hosts in *Malesia* include *Altingia*, *Ficus* and a species of *Loranthaceae*.

Note — Closely related to and sometimes difficult to distinguish from *V. articulatum*, differing in the flat, usually wider internodes, probably in having yellowish fruits, and possibly in the shorter rudimentary leaves. In contrast to *V. articulatum*, *Viscum nepalense* also apparently occurs commonly on hosts other than *Loranthaceae* or other *Viscaceae*. Danser in *Blumea* 4 (1941) 285 maintained the distinction between the two species, and commented on difficulty in discrimination. Slender specimens lacking fruit characters are difficult to place, especially in Java.

6. *Viscum ovalifolium* DC.

Viscum ovalifolium DC., Prodr. 4 (1830) 278; Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 48; *Blumea* 4 (1941) 296; Backer & Bakh. f., Fl. Java 2 (1965) 75. — Type: Wallich 489, Penang.

Viscum orientale auct. non Willd.: Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 466; Philipp. J. Sc. 58 (1935) 139.

Viscum pedunculatum Barlow, Proc. Linn. Soc. New S Wales 87 (1962) 58. — Type: Barlow 128, Queensland, Ellis Beach.

[For additional synonymy see Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 48; *Blumea* 4 (1941) 296].

Plant slender to robust, erect, to 1.5 m high. *Stem* internodes terete, sometimes flattened and double-edged upwards, 10–60 mm long, 1–4 mm wide below, widened to 2–5 mm above, striate or weakly ridged longitudinally. *Leaves* mostly normally developed; lamina narrowly elliptic to obovate, sometimes falcate when narrow, attenuate at the base to an obscure petiole 2–5 mm long, often undulate at the margin, rounded to acute and shortly mucronate at the apex, curvinerved, usually with 3 veins visible on both sides, 25–120 by 10–35 mm. *Inflorescence* axillary, sometimes produced on short lateral shoots lacking normally developing leaves and then appearing spicate, a pedunculate or sessile cymule of 3 flowers subtended by a cupule c. 1 mm long, usually with many subsidiary cymules developing around the first one, with the middle flower female and the lateral flowers male; peduncle 0–5 mm long. *Fruit* globose or slightly ellipsoid, usually attenuate at the base, sometimes on a stipe to 3 mm long, distinctly tuberculate before maturity, yellow, orange or red. — **Fig. 9b, 13.**

Distribution — From Burma eastwards to Hong Kong and southwards to northern Queensland; *Malesia*: widespread throughout the region.

Habitat & Ecology — Mostly in lowlands from 0 to 500 m altitude, less frequently to 1400 m, in mangroves and open and closed forests; recorded commonly on *Ficus*, but also on many other hosts.

Notes — 1. A polymorphic species, notably variable in the degree of flattening of the internodes, development of a stipe below the fruit, and length of the pedicel. This makes the clear distinction of *Viscum wrayi* difficult (see there). The occasional development of seemingly spicate inflorescences on leafless shoots gives a superficial resemblance to *Ginallia*, but fruit characters clearly show the identity.



Fig. 13. *Viscum ovalifolium* DC. Twig with warty ripe fruits. Photograph B. A. Barlow, 1982, macro-photograph from herbarium specimen. Reproduced with permission from Brunonia 6.

2. Both diploid ($n = 11$) and tetraploid ($n = 22$) chromosome races are known in *V. ovalifolium* [Wiens & Barlow, Taxon 20 (1971) 317; Barlow, Brunonia 6 (1983) 31, 33], and some of the polymorphy may be attributable to this differentiation.

7. *Viscum scurruloideum* Barlow

Viscum scurruloideum Barlow, Blumea 41 (1996) 344. — Type: *Hildebrand s. n.*, Java, Preanger.
Ginalloa falcata Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 451; Backer & Bakh. f., Fl. Java 2 (1965) 75. — Type: *Backer 10846*, Java, Nirmala.

Plant slender, probably pendulous. *Stem* internodes terete below, flattened upwards, longitudinally ridged, 25–60 mm long, 1–1.5 mm wide below, widened to 1.5–2 mm

above. *Leaves* normally developed; lamina linear, falcate, gradually attenuate at the base to an obscure petiole 2–5 mm long, attenuate and finally acute to rounded at the apex, curvinerved with 3 veins raised on both sides, 40–75 by 3–5 mm. *Inflorescences* terminal and axillary, a pedunculate cymule of 3 flowers subtended by a cupule c. 0.5 mm long, with the middle flower female and the lateral flowers female or male; peduncle 2–4 mm long. *Fruit* ellipsoid, on a distinct, slender stipe c. 5 mm long, smooth. — **Fig. 11 d–f.**

Distribution — *Malesia*: western Java.

Habitat & Ecology — 1000–1500 m altitude; the only recorded host is *Castanopsis javanica*.

Note — For discussion of transfer from *Ginallia* to *Viscum*, see Barlow, l.c.

8. *Viscum stenocarpum* Danser

Viscum stenocarpum Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 469. — Type: *Docters van Leeuwen 12160*, Java, Cibodas.

Viscum liquidambaricolum auct. non Hayata: Danser, Bull. Jard. Bot. Buitenzorg III, 16 (1938) 57, p.p.; Blumea 4 (1941) 289, p.p.; Backer & Bakh. f., Fl. Java 2 (1965) 75.

Plant slender to moderately robust, erect or pendulous, to 1 m long. *Stem* internodes terete or decussately flattened or compressed, quadrangular or double-edged, then usually with a raised angular rib on each face, usually distinctly longitudinally ribbed, 15–60 mm long, 0.5–1.5 mm wide below, widened to 1–2 mm above. *Leaves* rudimentary, spreading, 0.2–0.5 mm long. *Inflorescences* 1 or sometimes 2 in the axils, rarely with subsidiary cymules developing lateral to the first one, a sessile cymule of 3 flowers, subtended by a cupule 0.5–1 mm long, with the middle flower female and the lateral flowers male. *Fruit* ellipsoid to almost globose, sessile, smooth, yellow to red, often striate.

Distribution — *Malesia*: Sumatra, Java, Celebes; possibly Borneo.

Habitat & Ecology — Mostly 1000–1500 m altitude, rarely lower to 20 m, rarely higher to 2300 m; recorded hosts include *Altingia*.

Notes — 1. Similar to *V. articulatum*, differing in the often more nearly terete stems more prominently ribbed, the usual absence of subsidiary cymules, the shape and colour of the fruits, and probably in host preference.

2. Danser in Bull. Jard. Bot. Buitenzorg III, 16 (1938) 57 and Blumea 4 (1941) 289 reduced *V. stenocarpum* to synonymy with *V. liquidambaricolum* Hayata of mainland Southeast Asia, primarily on the similar fruit characters. The latter species has flattened internodes and in vegetative characters differs sharply from *V. stenocarpum* in the same way as *V. nepalense* differs from *V. articulatum* (see notes there). *Viscum stenocarpum* is accordingly treated as distinct from, although closely related to *V. liquidambaricolum*.

3. Two specimens seen from northern Borneo show a combination of characters of *V. articulatum* and *V. stenocarpum*, suggesting local introgression between these two species.

9. *Viscum wrayi* Gamble

Viscum wrayi King ex Gamble, Kew Bull. (1913) 47; Danser, Bull. Jard. Bot. Buitenzorg III, 11 (1931) 470; Blumea 4 (1941) 297. — Type: *Wray 1111*, Perak, Mt Batu Puteh, lecto.

Plant moderately robust, erect. *Stem* internodes compressed or flattened and double-edged, longitudinally ribbed, 25–50 mm long, 1–2 mm wide below, widened to 2–4 mm above. *Leaves* normally developed; lamina spatulate to obovate, attenuate at the base to an obscure petiole 2–4 mm long, dark and slightly lustrous on both surfaces, rounded at the apex, 25–50 by 12–25 mm, curvinerved with 3 or 5 veins obscure. *In-florescences* axillary and terminal, a pedunculate cymule of 3 flowers, subtended by a cupule c. 1 mm long, with subsidiary cymules sometimes developing adjacent to the first, with the middle flower female and the lateral flowers male; peduncle 1–3 mm long. *Fruit* globose or depressed-globose, on a stipe 2.5–4 mm long, usually smooth and shining, sometimes weakly tuberculate, with a short distinct neck, yellow-green to yellow-brown.

Distribution — *Malesia*: Sumatra, Peninsular Malaysia, Borneo.

Habitat & Ecology — Mostly in lowland humid forests from 200 to 1300 m altitude; recorded hosts include *Dendrophthoe*, *Gomphia* and a species of *Rutaceae*.

Note — Closely related to *V. ovalifolium*, which within its range of polymorphy occasionally exhibits most of the distinctive characters of *V. wrayi*. The latter can be distinguished on its combination of flattened double-edged stem internodes, spatulate or obovate lustrous leaves, shortly pedunculate triads, and globose stipitate fruits which are usually shining and only slightly tuberculate.

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ISBN 90-71236-33-1

Flora Malesiana

Compiled and published under the auspices of
Foundation Flora Malesiana

